

KOLPOCHOERUS PAICEAE (MAMMALIA, SUIDAE)
FROM SKURWERUG, NEAR SALDANHA, SOUTH AFRICA,
AND ITS PALAEOENVIRONMENTAL IMPLICATIONS

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(With 17 figures and 4 tables)

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ABSTRACT

A *Kolpochoerus* skull from a consolidated coastal dune at Skurwerug near Saldanha Bay is identified as an early Pleistocene representative of the southern African *K. paiceae* lineage. It is more primitive than the middle Pleistocene *K. paiceae* from the nearby Elandsfontein fossil site, and is in a comparable evolutionary state to 1,0 to 2,0 Ma *K. limnetes* from East Africa. Its suggested age is in accord with that of the high sea-level of the eustatic cycle Q2, during which the Skurwerug dune was apparently formed under circumstances similar to those that have influenced the formation of the nearby late Pleistocene-Holocene Spreeuwal dune plume. The Skurwerug *K. paiceae* suggests the presence of woodland or forest patches in the Saldanha region during the early Pleistocene.

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INTRODUCTION

During 1979, the South African Museum acquired a small collection of fossil mammals from a large excavation that was being undertaken in a consolidated calcareous dune at Skurwerug, near Saldanha in the south-western Cape Province (Fig. 1). Access to the excavation was restricted for security reasons and it was not possible to determine the nature of the fossil occurrence, or to undertake a systematic investigation of the deposits from which the material was derived.

Such occurrences are not uncommon in the region and the Skurwerug specimens would have been of little interest and significance but for the fact that the collection included a particularly fine skull of an extinct pig. This specimen was found by Mr Albert W. Abraham and donated to the South African Museum by Mr P. Hutton. Other fossils from the Skurwerug excavation, which are all in a fragmentary state, were not necessarily associated with the pig skull and they will not be considered in detail here. The mammals include *Equus* cf. *capensis*, *Connochaetes* sp., *Gazella* sp. and *Raphicercus* sp.

As soon as the specimen was received it was recognized that the general morphology of the skull and cheek teeth served to place the specimen in the genus *Kolpochoerus* (formerly *Mesochoerus*) and the third molars were comparable in size with material from East Africa assigned to *K. limnetes* (Cooke 1976; Harris & White 1979). The marked reduction in the premolars indicated affinity with *K. paiceae* from South Africa but the third molars are smaller than in the large sample from Elandsfontein, suggesting that the Skurwerug specimen may be an early form of this lineage. Despite the lack of a detailed account of this specimen, it has come to be accepted as indicative of an early Pleistocene age for the coastal dune from which it was derived (Hendey 1981a, 1983a; Rogers 1982, 1983). It is the purpose of this paper to identify and describe the specimen and to consider its implications in respect of the geological succession and palaeogeography of the Saldanha region.

SYSTEMATICS AND DESCRIPTION

ORDER ARTIODACTYLA

Family Suidae

Genus *Kolpochoerus* van Hoepen & van Hoepen, 1932

Type-species: Kolpochoerus sinuosus van Hoepen & van Hoepen, 1932 (= *Kolpochoerus paiceae* (Broom, 1931)—see Cooke (1978)).

Discussion

Material assigned to *Kolpochoerus* has been recovered from many late Pliocene to middle Pleistocene localities in Africa, and it has been reviewed in recent publications by Cooke (1978), Cooke & Wilkinson (1978), White & Harris (1977), Harris & White (1979), and Harris (1983). The latter authors recognized only two valid species, whereas Cooke distinguished five. Many pig genera and species recorded prior to 1977 have been synonymized with *Kolpochoerus* and with the few species recognized by those authors cited above. The earlier nomenclatural proliferation, and the subsequent difference of opinion on the number of valid species, was due at least in part to the variation in dental characters exhibited by *Kolpochoerus* populations over its three-million-year time range so that recorded material represents temporal and, apparently, also regional variants.

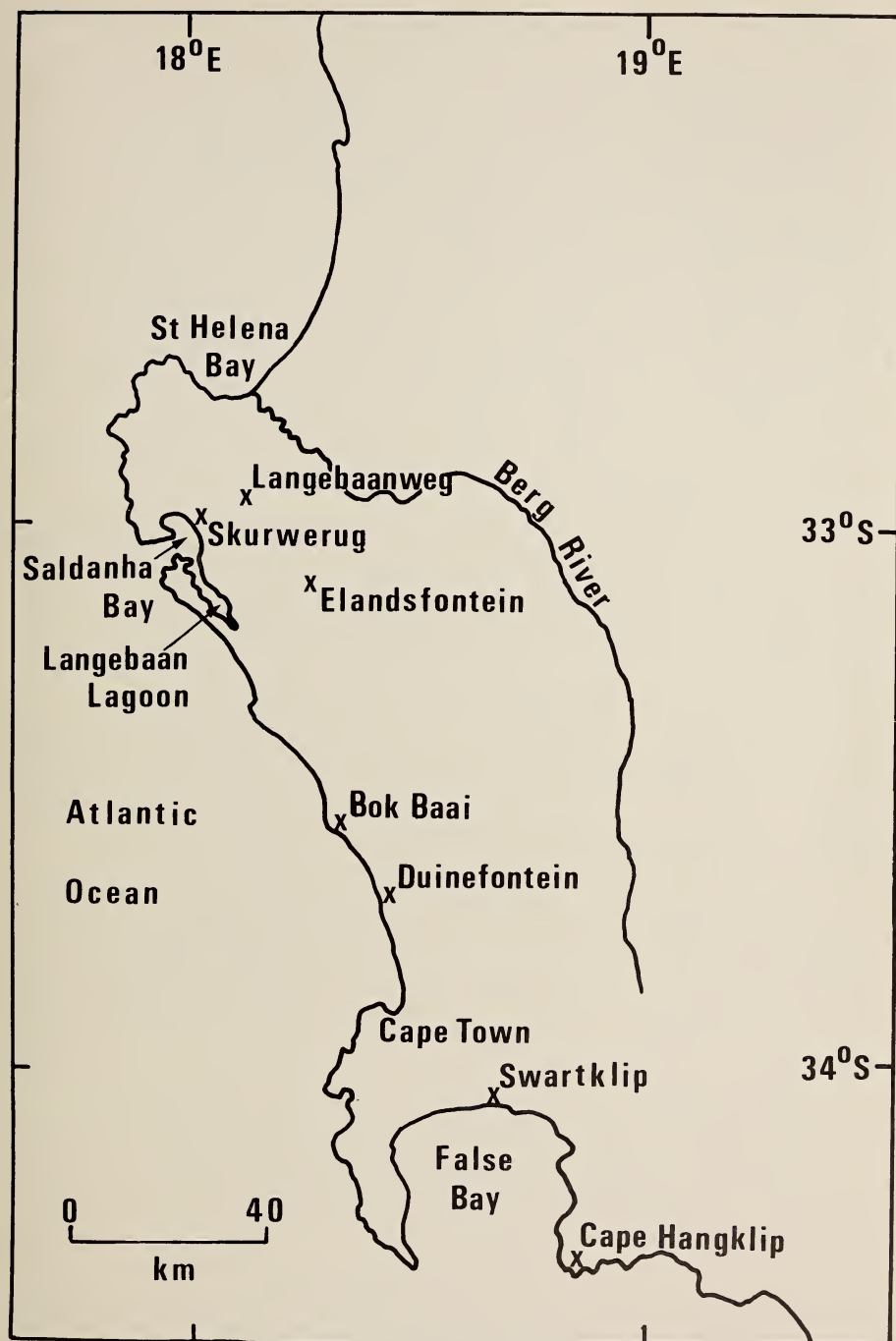


Fig. 1 The location of Skurwerug.

The only two species recognized by Harris & White (1979) are *K. limnetes* and *K. majus*. Of these, *K. limnetes* is considered to be represented by a continuum from an early form with small third molars to an 'advanced' form with elongate third molars. However, Cooke (1976, 1978) regards the advanced form as a separate species, *K. olduvaiensis*, but it would be inappropriate to debate this matter here as it is the taxonomy and not the morphology that is in question. Accordingly, to avoid unnecessary confusion in the present account, 'typical' *K. limnetes* refers to the material ascribed to this species both by Cooke and by Harris & White, while 'advanced' *Kolpochoerus* (without a species designation) denotes the advanced *K. limnetes* of Harris & White or the *K. olduvaiensis* of Cooke. *Kolpochoerus 'majus'* is contemporary with the 'advanced' *Kolpochoerus* but the third molars are in the size range of the 'typical' *K. limnetes*; they differ in being relatively more hypsodont, have more crenulated enamel and the crowns of the teeth have a distinctive lateral bulge just above the enamel line. Cooke & Wilkinson (1978) consider that the name '*majus*' is a *nomen vanum* but they recognize the reality of this entity.

One of the differences of opinion referred to above concerns the recognition by Cooke (1976, 1978) of a South African lineage that is represented by the species *K. paiceae*. This species is recorded from middle Pleistocene occurrences at Elandsfontein, Cornelia, the Vaal River gravels (Cooke & Wilkinson 1978), and in Zululand (McCarthy & Orr 1978). It has hitherto been known from only fragmentary specimens, with the largest assemblage coming from Elandsfontein, which is 20 km south-east of Skurwerug (Fig. 1). This material does not show the distinctive characteristics of *K. 'majus'* but there has hitherto been only slender evidence for distinguishing it from the 'advanced' *Kolpochoerus* of East Africa. Harris & White (1979) believe that until there is an unequivocal separation of *K. paiceae* and *K. limnetes* on dental and cranial evidence, *K. limnetes* should stand as the senior synonym of a single species.

It cannot be expected that the discovery of the remains of a single individual, no matter how complete and well preserved, would settle the status of *K. paiceae*, but the Skurwerug specimen does lend support to Cooke's belief in a South African *Kolpochoerus* lineage. This specimen is evidently a more primitive form than that recorded from Elandsfontein, but it is very similar in some respects to specimens in the Elandsfontein assemblage, and to the type material from the Vaal River gravels; it is accordingly identified with *K. paiceae*.

In the final analysis, the specific identity of the Skurwerug *Kolpochoerus* is not critical since its significance lies chiefly in indicating a somewhat earlier presence of this taxon at the southern extremity of Africa than has been known hitherto, with corresponding implications in respect of the relative dating of the deposits from which it was derived.

Kolpochoerus paiceae has been known hitherto only by its dentition and by parts of the mandible so the skull characters of SAM-PQ2166 must be considered in relation to the skulls from East Africa. The general morphology of the East African material has been discussed in several papers (e.g. Cooke & Wilkinson

1978; Harris & White 1979), with the latter publication including illustrations of several specimens. These are KNM-ER 409 (pl. 10, centre, pl. 12, top), KNM-ER 212 (pl. 12, left), KNM-ER 772 (pl. 10, top), KNM-ER 788 (pls 8, 9) and KNM-ER 1085 (pl. 10, bottom), all from the Koobi Fora succession. The first two are reasonably representative of the male skull, though they are larger than the few cranial specimens from the Shungura Formation, still undescribed (Cooke & Coppens in press). KNM-ER 778 and 772 came from the upper part of the Koobi Fora succession ('*Metridiochoerus compactus*' zone) and represent the large 'advanced' *Kolpochoerus* that Cooke & Wilkinson (1978) regard as a distinct species, *Kolpochoerus olduvaiensis*. Female cranial remains are rather rare and the only female of *K. limnetes* so far illustrated is the incomplete specimen KNM-ER 1085, apart from a rather crushed skull of this species from Bed I, Olduvai (KNM-OLD FLK NNI 1235), formerly the type of *Ectopotamochoerus dubius* (Leakey, 1965, pl. 25). An almost intact undescribed large cranium from Peninj, Lake Natron, has been regarded by Cooke & Wilkinson (1978) as the female of *Kolpochoerus olduvaiensis*. Sexual dimorphism is strong, with the female having lesser development of the zygomatic arches and smaller canine flanges than in the male. The degree of difference is comparable with, or greater than, that seen in the forest hog *Hylochoerus meinertzhageni*, which is apparently the closest living relative of *Kolpochoerus* although it has special features of its own (Cooke 1976; White & Harris 1977).

Kolpochoerus paiceae (Broom, 1931)

Notochoerus paiceae Broom, 1931: 167, fig. 1

Kolpochoerus sinuosus van Hoepen & van Hoepen, 1932: 59, figs 72, 75-77. Cooke, 1974: 73, fig. 5.

Notochoerus capensis Shaw, 1939: 85, fig. 8 (*partim*).

Mesochoerus paiceae Shaw & Cooke, 1941: 293, pl. 54 (1-2). Cooke, 1949a: 35, figs 18, 19; 1949b: 44, pls 22, 23; 1976: 253, fig. 1. Keen & Singer, 1956: 352, pl. 33E. Leakey, 1958: 13. Cooke & Maglio, 1972: 310.

Metridiochoerus andrewsi Arambourg, 1943: 473 (*partim*); 1947: 352, fig. 42 (*partim*).

Tapinochoerus meadowsi Cooke, 1949a: 31, fig. 15 (*partim*).

Mesochoerus lategani Singer & Keen, 1955: 170, fig. 1. Keen & Singer, 1956: 350, pl. 33A-D. Cooke & Maglio, 1972: 310.

Kolpochoerus paiceae Cooke, 1978: 460. Cooke & Wilkinson, 1978: 462.

Mesochoerus limnetes Harris & White, 1979: 37 (*partim*).

Diagnosis

A species of *Kolpochoerus* comparable in size with the living forest hog and similar in skull size and general morphology to the 'typical' *K. limnetes* of East Africa, from which it differs in the following: relative reduction in the length of the snout and symphysis; relative elevation of the occipital condyles above the palatal plane, accompanied by reduction in height of the occiput; slight elevation of the orbits; mandibular corpus very robust; anterior border of symphysis very gently curved, resembling that of *Hylochoerus*; three pairs of lower incisors but upper reduced to two pairs; three reduced upper premolars and only two lower premolars. Third molars comparable in size and structure to those of 'advanced'

K. limnetes (*sensu* Harris & White 1979) or *K. olduvaiensis* (*sensu* Cooke & Wilkinson 1978). Male upper canines shorter and more strongly curved than in normal *K. limnetes*; female canines small but with normal open roots.

Holotype

Mandible fragment with right third molar and stump of second molar, from Vaal River gravels, Windsorton, Cape Province. McGregor Museum, Kimberley, MMK 4088.

New material

SAM-PQ2166: the incomplete skull and mandible of an adult, lacking the anterior parts of the nasals, some of the premaxillae and maxillae, all of the right and parts of the left zygomatic arches, left I², right P², left ascending ramus and left I₃.

Locality and horizon

Skurwerug, a consolidated dune on the farm Osfontein, 2 km inland from the eastern shore of Saldanha Bay in the south-western Cape Province. This dune is included in the Langebaan Limestone Member of the Bredasdorp Formation, as it is defined by Rogers (1983).

Description

The Skurwerug skull is that of an adult, probably female, in which all the permanent teeth are erupted, with only the most posterior pillars of the M³ talon being unworn. In size it is comparable with that of the forest hog and smaller than the male specimens from the Shungura Formation, which, in turn, are smaller than those from Koobi Fora.* Principal measurements are given in Table 1* in comparison with the earliest of the Omo male crania, L193-109 from Shungura Member C8, the smallest (KNM-ER212) and the largest and most advanced (KNM-ER788) of the male crania from the Koobi Fora Formation. Also included are applicable measurements for the partial female cranium KNM-ER1085 from Koobi Fora and for the large undescribed female cranium from West Natron (Peninj),* numbered A67-384 in the collections of the National Museum of Tanzania, Dar-es-Salaam. It should be noted that these specimens cover a substantial time range.

Cranial morphology (Table 1; Figs 2, 3)

In profile the Skurwerug cranium shows the marked angulation between the rostral region and the frontals that is characteristic of *Kolpochoerus*. The back of the braincase is not unduly elevated but the occipital condyles are much higher above the palatal plane than is the case with 'typical' *K. limnetes* and this

*Personal observations by HBSC, as also are all measurements cited for East Africa; there may be minor differences from measurements given by Harris & White (1979) or by Harris (1983) but they are insignificant.

elevation is accompanied by reduction in the height of the occiput itself. This is a unique feature not seen in other specimens. The braincase itself is very slightly concave between the orbits with the orbital rim rising just above the level of the frontals, whereas in the 'typical' form they are normally below it. The cranial vault is very gently convex and broad above the temporal fossae and the temporal ridges are not strongly marked. However, the doming is less than in the 'typical' *K. limnetes* but the vault is not depressed as it is in the males of the advanced form. The morphology is very similar to the condition seen in the Peninj cranium, which suggests that there may be a sexual difference comparable to that in the living forest hog. The supra-orbital foramina are in line with, or even slightly in front of, the anterior margins of the orbits, as in the 'typical' form, whereas in the advanced form these foramina are situated a little farther back.

Although the right zygomatic arch is lost and the left one is damaged, it is clear that there was no great lateral expansion as in the males of *K. limnetes*, in which the anterior margin sweeps outwards sharply until it is more or less perpendicular to the sagittal axis. In PQ2166 the form of the zygoma is like that of the Koobi Fora female ER 1085 and not as abruptly protuberant as in the Peninj female; indeed it is rather reminiscent of the zygoma of *Sus*, although more expanded laterally. The ventral margin must have been well above the occlusal plane, so there was little of the lateral 'droop' that is seen in the early males of *K. limnetes*.

The snout is damaged and the tips of the nasals are missing but the nasal on the right side is preserved to the level of the canines. It is strongly arched in transverse section along its preserved length. The nasals were widest above the back of the canine flange and there is a distinct, but not strong, lateral projection of the nasal-maxillary junction over the infra-orbital region. In males of early *K. limnetes* the lateral projection is marked and is often accompanied by the development of rugose areas on the nasal and adjoining maxillary similar to those found in males of *Potamochoerus porcus*. These rugose areas have not been noted in the later *K. limnetes*, although the overhang persists until it disappears effectively in the advanced form. There is no sign of any rugosity in the Skurwerug specimen, as is to be expected in a female.

The right canine flange is lacking and the left one is damaged but sufficient remains to show that it was weakly developed in comparison with the strong *Potamochoerus*-like bosses seen in 'typical' male *K. limnetes*. The flange in PQ2166 curves gently out from the maxilla well in front of the infra-orbital foramen and is intermediate in form between those of female *Potamochoerus* and female *Hylochoerus*. There is a weak lateral crest about 20 mm in length that arises some 25 mm from the root of the flange at the maxilla but the flange is not at all inflated. No trace exists of any dorsal crest and it was probably absent. The canine is moderately small and emerges more or less parallel to the palatal surface. In the female cranium ER 1085 the canine flange is also small but has a marked lateral crest and there is a more prominent gutter between the front of the flange and the wall of the maxilla. In the Koobi Fora female the canine itself was



Fig. 2. Dorsal, lateral and ventral views of the *Kolpochoerus paiceae* skull from Skurwerug (SAM-PQ2166).

TABLE 1
Dimensions (in mm) of the Skurwerug cranium, SAM-PQ2166,
and some other *Kolpochoerus* crania.

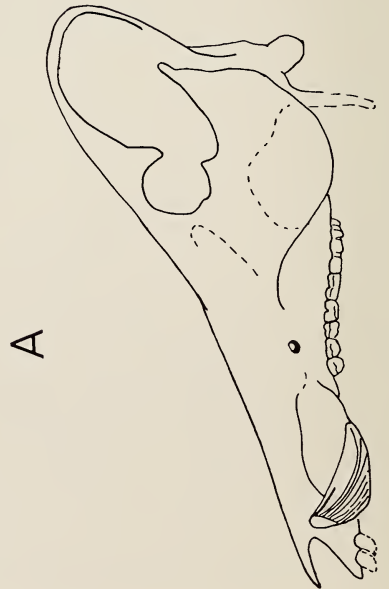
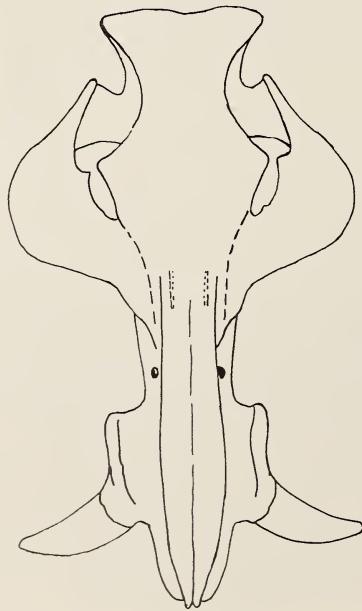
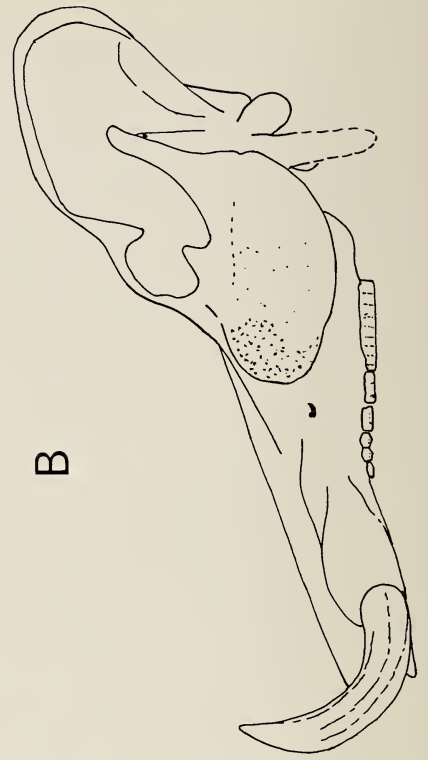
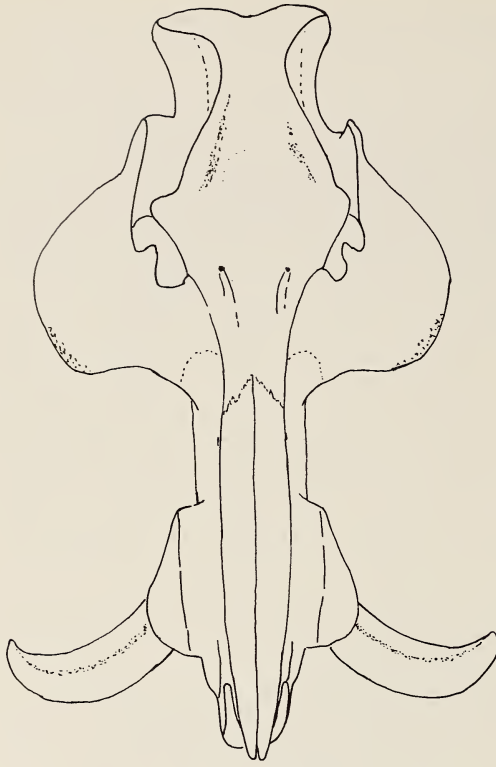
Locality	Skurwerug	Peninj	Koobi Fora			Omo
Sex	♀	♀	♀	♂	♂	♂
Number	PQ2166	A67-384	ER 1085	ER 212	ER 788	L193-109
Estimated age (Ma)	?	c. 0,9-1,3	?*	?*	1,5	2,5
Vertex length	425	553	—	505e	602	465e
Basilar length	375e	465	—	436e	483	c. 400e
Palatal length	263e	341	c. 270e	325e	354	c. 280e
Bizygomatic breadth	260	318e	—	278	364	c. 290e
Crest breadth	112	c. 150e	—	132e	145	120e
Parietal constriction	46	62e	—	65,5e	48,5	56e
Frontal breadth	134	143e	—	133	159	123e
Ocular breadth	104	125	90	108,5	110	105
Maxillary breadth at M ³	87,5	104,5	82	83	101,5	96
Post-canine breadth	c. 57	74	58e	79	84	76,5
Flange breadth	113e	123e	108e	140	180	150e
Precanine breadth	c. 78	71	—	73e	91,5	—
Height of occiput	131	212e	—	183,5	203	175e

c. = approximate; e = estimated

*The horizons for ER 1085 and ER 212 are not certain but the age is probably about 2,0 Ma ($\pm 0,5$ Ma).

also directed less laterally and slightly downwards relative to the palatal plane. In the Peninj cranium the flanges are damaged but were essentially similar except that they are distinctly tapered towards the canine root area. At the canine alveolar margin in ER 1085 the opening is about 17 mm wide and 15 mm high compared with 23 mm and 19 mm in the Skurwerug cranium; in the Peninj cranium approximate estimates are 28 mm and 23 mm respectively. In all three cases the canine had a strong dorsal groove.

The palate in 'typical' *K. limnetes* resembles that of the forest hog in general but is proportionally a little narrower. The tooth rows are usually slightly curved so that the palate is widest between the second molars and narrowest at the third molars; the anterior premolars may curve gently outwards beneath the expanded canine flanges. In PQ2166 the palate broadens anteriorly from M², much as in *Hylochoerus*. The palatine foramina, which normally lie level with the anterior pillars of M³, are slightly farther back in the Skurwerug cranium. There are two specimens of the Elandsfontein *K. paiceae* in which the palatine foramen is preserved. In one (SAM-PQ-ES5) it is positioned as in PQ2166, but in the other (SAM-PQ-ES20) it is even more posteriorly situated, being opposite the posterior pillars of the M³ trigon (Singer & Keen 1955, pls 23A, 24A). In the female cranium from Koobi Fora, KNM-ER 1085, and also in the Peninj female cranium, the palatine foramina are level with the front of M³, so this is not merely a sexual difference. In the palate of PQ2166, the U-shaped palatonarial border is situated only a short distance behind M³, which is apparently a primitive



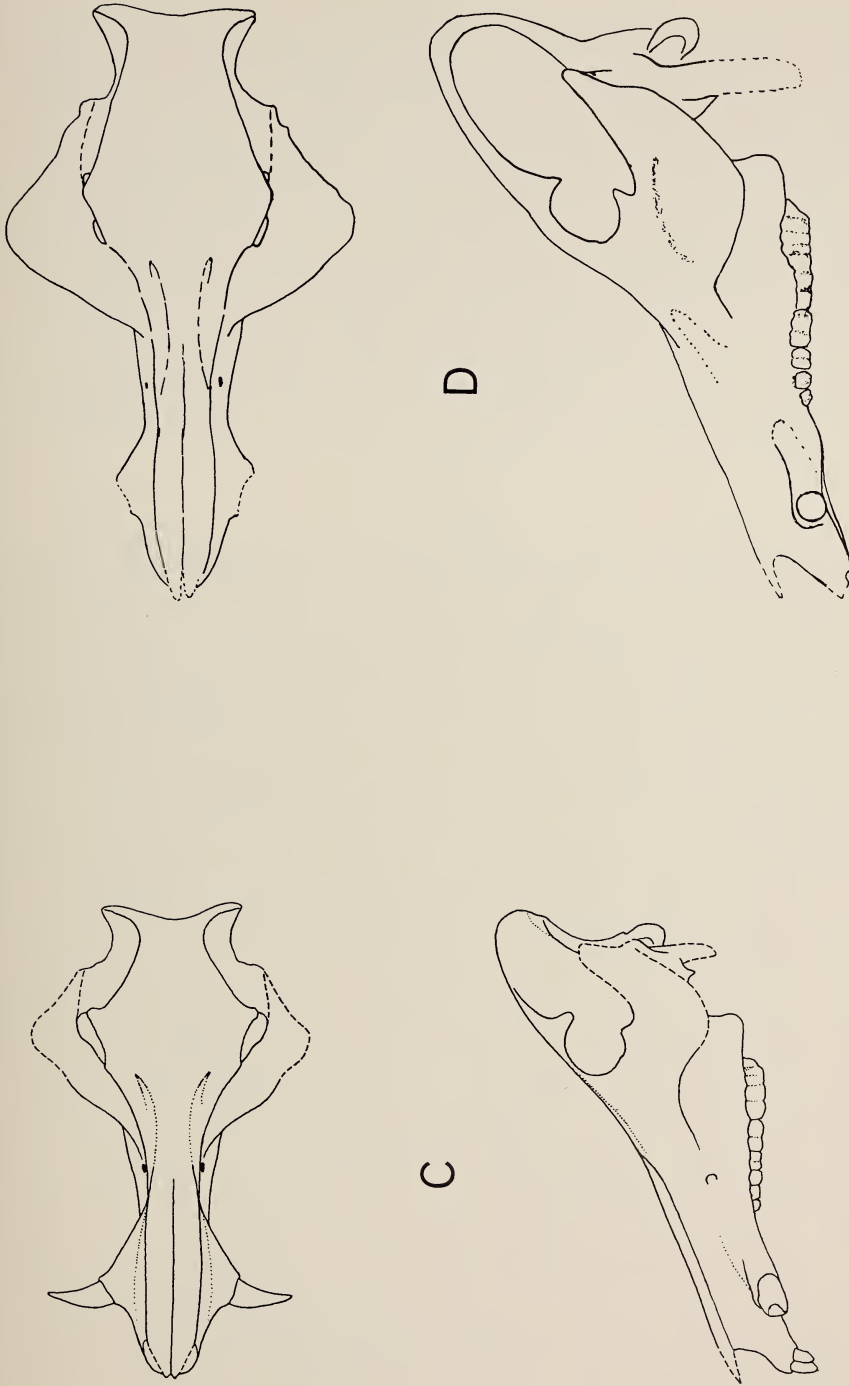


Fig. 3. *Kolpochoerus* skulls. A. 'Typical' *Kolpochoerus limnetes* (KNM-ER 409). B. 'Advanced' *Kolpochoerus limnetes* (= *olduvaiensis*) (KNM-ER 788). C. *Kolpochoerus paiceae* (SAM-PQ2166). D. 'Advanced' *Kolpochoerus limnetes* (= *olduvaiensis*) female (Penini).

characteristic, since according to Harris & White (1979) this distance is increased in advanced specimens. In the Koobi Fora female the palatonarial border is very much in the same position as in the Skurwerug cranium whereas in the Peninj cranium it extends much farther back.

The premaxilla is usually badly damaged but it is partially preserved in a few specimens of 'typical' *K. limnetes*, in the advanced Koobi Fora KNM-ER 788, KNM-ER 772 and in the Peninj cranium. It is subtriangular in shape with a rounded apex and the three incisors on each side lie almost in a straight line one behind the other as in *Sus* or *Potamochoerus*. I³ is small but is normally retained into old age, although in KNM-ER 772 it was shed during life. In PQ2166 the premaxilla is shorter and broader with a more arcuate border, only two premolars are present on each side and I² is more laterally situated in relation to I¹. There is no trace of I³ or of any scar. The I¹ and I² are essentially similar in morphology to the corresponding teeth of *Potamochoerus porcus* and to teeth attributed to *K. limnetes*.

Upper canines

The upper canines of 'typical' male *K. limnetes* somewhat resemble those of *Hylochoerus* but are shorter and relatively stouter, curving laterally at the tips with less of a backward or upward sweep than in the forest hog. There is a broad wear facet cutting across the front of the tooth. In structure the canines are also like those of *Hylochoerus*, with a strong dorsal longitudinal groove and shallower grooves on the anterior and posterior surfaces. There is a robust ventral band of ribbed enamel, a narrow inset band of smooth enamel on the anterior edge of the tusk and another on the posterior face, about 1 cm above the rear ridge of the ventral band. In *Hylochoerus* the diameter of the tusk is greater in the vertical direction whereas in *Kolpochoerus limnetes* the dimensions are about equal or the tusk is dorso-ventrally flattened. In the few specimens attributed to females, the canines are smaller, emerge with a downward and lateral component and taper at the base to form closed or nearly closed roots. The teeth are less curved than in males and the tip is cut by a small wear facet. In unworn teeth the tip of the female canine is covered with thick enamel but it thins posteriorly, extending farthest on the ventral side whereas on the dorsal side a V-shaped area of dentine extends towards the tip, coinciding with a dorsal groove in the root area. There is a good sample of both male and female canines from Olduvai Bed I in which the female canines measure about 9–10 cm in length from tip to root and the maximum and minimum diameters of the cross-section are 19–22 mm by 12–16 mm; the male canines are 20–25 cm in length, have open root areas, and cross-section diameters in the range 29–45 mm with the vertical measurement sometimes greater than the antero-posterior diameter. Male canines from the Shungura Formation up to Member G are about the same size, as also are those of 'typical' *K. limnetes* from Koobi Fora. In advanced *Kolpochoerus* the canines are longer (c. 30–35 cm) and stouter (50 mm by 39 mm in ER 788).

The canines of the Skurwerug cranium project 5 cm from the alveolar margin and the root area may occupy about another 4–5 cm. The curvature is fairly sharp and they are directed forwards and laterally almost in the palatal plane. At the alveolar margin the antero-posterior diameter is close to 24 mm and the dorso-ventral diameter 19–20 mm. There is a strong dorsal groove and weaker anterior and posterior grooves, as well as a strong ventral band of very weakly grooved enamel. There is nothing to suggest that the roots are closed. The tips are cut by a moderately broad wear facet. The size and form of these canines is thus a little more 'masculine' than are the Olduvai teeth, yet both in size and in structure they fall short of being typically male. This may be taken as indicating a degree of sexual dimorphism less marked than in 'typical' *K. limnetes* or even in the 'advanced' *Kolpochoerus* represented by the Peninj female. On the other hand, the convergence in structure is not quite as great as in female *Hylochoerus*.

TABLE 2

Dental dimensions of *Kolpochoerus paiceae* specimen, SAM-PQ2166 from Skurwerug.

	Upper		Lower	
	Left	Right	Left	Right
Length premolar series	31,2	33e	26,5	26,5
Length molar series	91,5	94,2	99,9	99e
Length cheek teeth series	123	126e	124,3	124,5e
Canine—antero-posterior diameter	24,5	23,5	21,6	22,4
—dorso-ventral diameter	18,9	20,1	18,1	18,3
—length from alveolus	51	52	67e	67
Diastema C—P ² /P ₃	47	—	57e	55,8
P2—Length (L)	8,2	lost	absent	absent
—Breadth (B)	5,0	—	—	—
—Height (H)	3,7 ⁺	—	—	—
P3—L	11,5	12,5	11,2	11,0
—B	11,0	10,3	7,0	6,9
—H	6,3 ⁺	7,4 ⁺	7,0 ⁺	8,0 ⁺
P4—L	10,7	10,3	15,2	14,6
—B	13,3	13,0	11,1	11,0
—H	5,9 ⁺	7,5 ⁺	9,0 ⁺	8,5 ⁺
M1—L	17,0s	17,4	15,9	c. 16,0s
—B	16,3s	15,2	c. 13,8	c. 14,0s
—H	d	2,5d	3,0d	3,5d
M2—L	23,0	22,2	23,7	23,2
—B	20,7	19,9	17,8	17,8
—H	20,0 ⁺	12,5 ⁺	8,5 ⁺	8,0 ⁺
M3—L	50,0	53,1	60,2	60,0e
—B	25,0	24,1	29,2	29,7
—H	25,0	25,0	21,0	22,0
—Trigon(id) length	28,7	29,8	29,2	29,7

c. = approximate; e = estimated; s = stump; d = mainly dentine

⁺ = incomplete (worn)

Upper cheek teeth (Table 2; Figs 2, 4, 5)

The upper dentition of the Skurwerug cranium is remarkable not only in having the incisors reduced in number (to two pairs) but also in having the premolars reduced both in size and in number (to three upper and two lower pairs). The Peninj cranium has the upper premolars reduced to only two pairs, but they are relatively enlarged rather than reduced. PQ2166 shows no sign of P¹, nor of any scar to indicate that it was ever present. In *K. limnetes* P¹ was present in the rare female specimen KNM-ER 1085 (although only the socket remains) and in the Olduvai Bed I palate FLK W 626, so its retention may well have been a normal feature in the 'typical' female. Although it is lacking in many of the male specimens, it is certainly present in some cases. At Olduvai it occurs in a crushed male skull FLK NN I 177, lying 0,5 cm in front of P², as in the female skull mentioned above; at Koobi Fora it was present in the male skull KNM-ER 212, lying in contact with P²; and in the Shungura Formation was present in the male cranium L193-109 from Member C8, lying 2,5 cm in front of P².



Fig. 4. Occlusal view of the left upper cheek teeth of the *Kolpochoerus paiceae* skull from Skurwerug (SAM-PQ2166). Natural size.

The P² of PQ2166, which is preserved on the left side only, has the exposed parts of its two roots fused. The normal P² has three cusps, one behind the other, with the central cusp the largest. In PQ2166 there are only two cusps, well fused and worn so that the dentine areas almost merge. The anterior cusp is longer than the posterior one and tapers anteriorly, giving it a triangular outline in occlusal view. It somewhat resembles the P¹ of other specimens although the true P¹ is single-rooted.

The right P³ is intact, that on the left slightly damaged, and both are well worn. The tooth is triangular in occlusal view, with one root anteriorly and two roots posteriorly. There is a large main cusp (paracone) on the labial side, another postero-lingually (hypocone), and a very small cusp posteriorly. An apparently small distinct cusp anteriorly has been linked to the central cusp

through wear. The rather *Sus*-like arrangement is normal for *Kolpochoerus limnetes* but the tooth is considerably smaller than in any of the other material referred to this species (Fig. 5).

The P⁴ has a more complex crown, with an almost molariform morphology. It apparently has three roots, and the tooth is broader posteriorly. The crown morphology is somewhat obscured by wear and is most clearly seen in the right P⁴. There are two pairs of more or less equally sized cusps anteriorly and posteriorly, and a small accessory cusp situated medially on the lingual side. There is a posterior cingulum. The enamel of the principal cusps is slightly crenulated. The teeth of 'typical' *K. limnetes* are normally dominated by the enlarged paracone and protocone with a lesser metacone; cingular cusps are commonly developed and add to the complexity of the pattern but the essentially quadritubercular pattern seen in the Skurwerug dentition has not been noted in the East African material. The P⁴ is substantially smaller than in any of the East African specimens (Fig. 5).

Both left and right M¹ of PQ2166 are heavily worn and details of their cusp morphology are no longer discernible. However, it is clear that this more or less rectangular tooth has paired roots anteriorly and posteriorly that supported paired cusps in an arrangement that is typical of the M¹ of *Kolpochoerus* and other pigs.

The M² of PQ2166 also has a typically *Kolpochoerus* morphology. This tooth has paired roots anteriorly and posteriorly, supporting paired cusps that are separated by a smaller median cusp, and flanked anteriorly and posteriorly by well-developed cingula that are fused with small median cusps. In size both M¹ and M² lie near the bottom of the range of East African *K. limnetes* material (Fig. 5).

In PQ2166, the M³ have the pillar-like structure that is characteristic of *Kolpochoerus*. The trigon is morphologically similar to M², and consists of two sets of paired cusps separated by a smaller median cusp, an anterior cingulum that is fused to a small median cusp, and another small median cusp posteriorly. The trigon cusps are crenulated. The talon is shorter than the trigon and its cusps are less symmetrically arranged. The most anterior of the talon cusps is a median one that abuts the posterior median cusp of the trigon. It is flanked by a smaller buccal cusp and a more posteriorly situated and larger lingual cusp. This arrangement is repeated in a second row of slightly smaller cusps. Finally, there is a single postero-buccal cusp on the left M³. There is no crenulation of the talon cusps. The M³ has a heavier cement cover than M². In size the teeth are appreciably smaller than all of those from Elandsfontein and fall well within the range for the sample from Olduvai Bed I (Fig. 5), or that from the Shungura Formation, Member G.

Mandible

The general form and characteristics of the mandible of PQ2166 conform to those seen in 'typical' *K. limnetes* but there are differences in the shape and proportions of the symphysis and in the reduction of the premolars in the

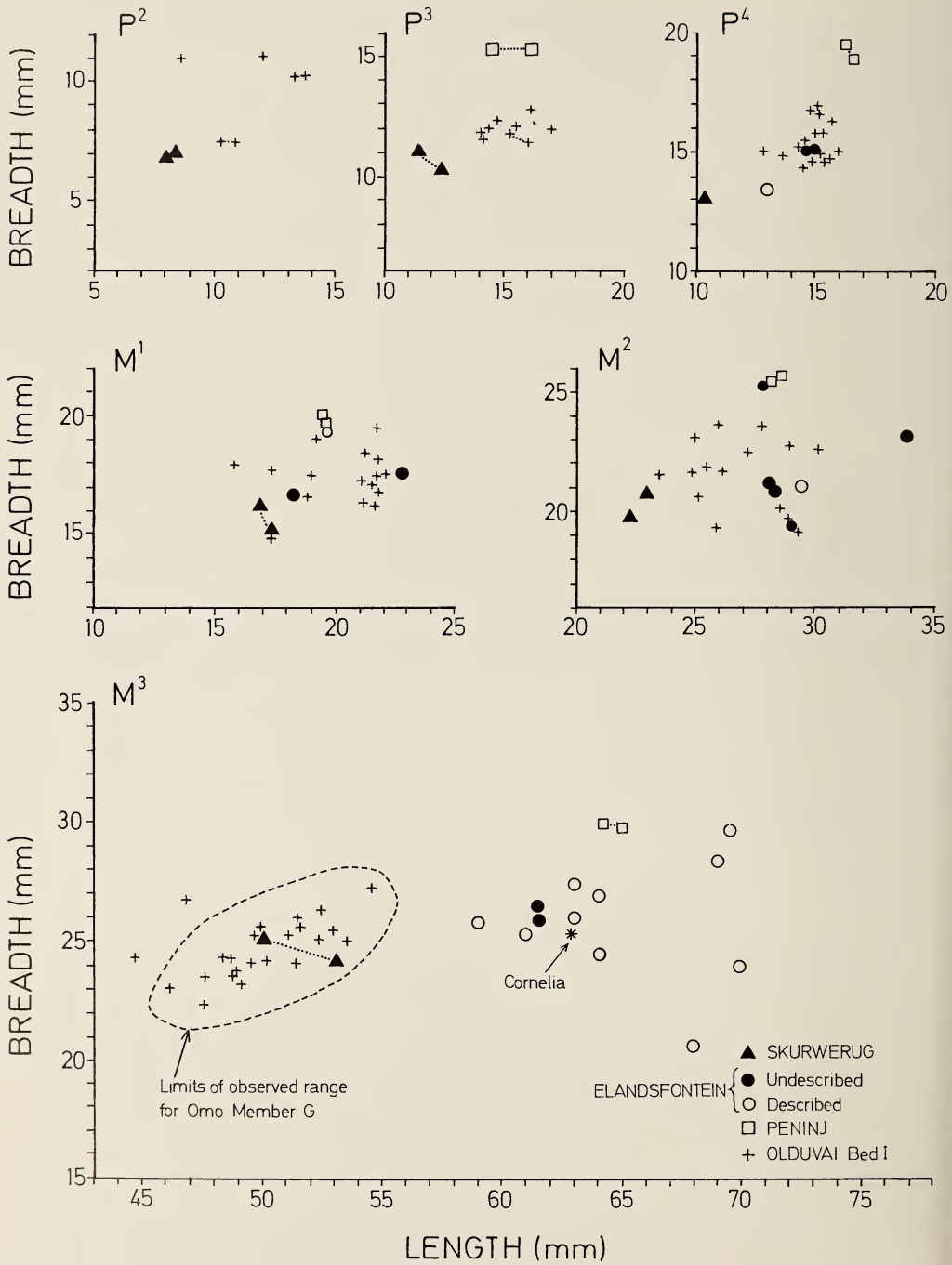


Fig. 5. Length/breadth measurements of upper cheek teeth of *Kolpochoerus paiceae* from Skurwerug, Elandsfontein and Cornelia, *K. limnetes* from Olduvai Bed I, and an advanced *Kolpochoerus* from Peninj.

TABLE 3
Dimensions of the Skurwerug mandible, SAM-PQ2166,
and some other *Kolpochoerus* mandibles.

Locality Number	Skurwerug		Elandsfontein		Olduvai		Koobi Fora		Omo	
	PQ2166	E20928	E16675	BM.M 17079 MMK III/IV	1000 FLK NN I	ER 946	ER 1314	OMO 27-3	OMO L64-5	
Estimated age (Ma)	?	c. 0,8	c. 0,8	c. 0,8	1,8	c. 1,7	?	2,0	2,5	
Total length	352	—	—	416	—	461	355	—	—	
Height of condyles	146	—	—	—	—	194	184	—	—	
Length of symphysis	101	c. 106	c. 106	139	115	146	125	145	114	
Canine flange breadth	93,5e	110e	102	136	92	129,5	104	129	112	
Constriction	73,5	95	86	92	73	101	93	97,5	85	
Jaw height at P ₄ /M ₁	64,5	68e	c. 66	76,5	57	65,5	61	c. 65	64,5	
Jaw thickness at M ₂ /M ₃	44	55	56e	43	43	55	46	c. 55	51	
Diastema C-P	56	62e	75e	91	62	96	81	69	85	
Premolar series	26,5	25e	c. 25	29+	38	42,5	41	46,5	42,5	
Molar series	99,9	c. 110	—	122,6	87,8	111	104	106	99,6	

c. = approximate; e = estimated



Fig. 6. Lateral and dorsal views of the *Kolpochoerus paiceae* mandible from Skurwerug (SAM-PQ2166).

Skurwerug specimen. *Kolpochoerus* shares with *Hylochoerus* a stout mandible with great width across the canines, only modest constriction behind them, and inflation of the corpus lateral to P₄, narrowing again fairly abruptly opposite the middle of M₃. In *Hylochoerus* the mandible of the female is a little less robust than in the male but the differences are slight. In the forest hog the breadth across the canines is about the same as the length of the symphysis—relatively slightly narrower in females—whereas in *Kolpochoerus limnetes* the symphysis is longer than the breadth across the canines. In the forest hog the back of the symphysis lies well in front of the anterior premolar and the gap between it and the back of the canine is about equal to the sum of the lengths of the three molars; in 'typical' *K. limnetes* the symphysis begins about level with the anterior premolar and the gap is about as long as the third molar, or a little longer. In the forest hog the

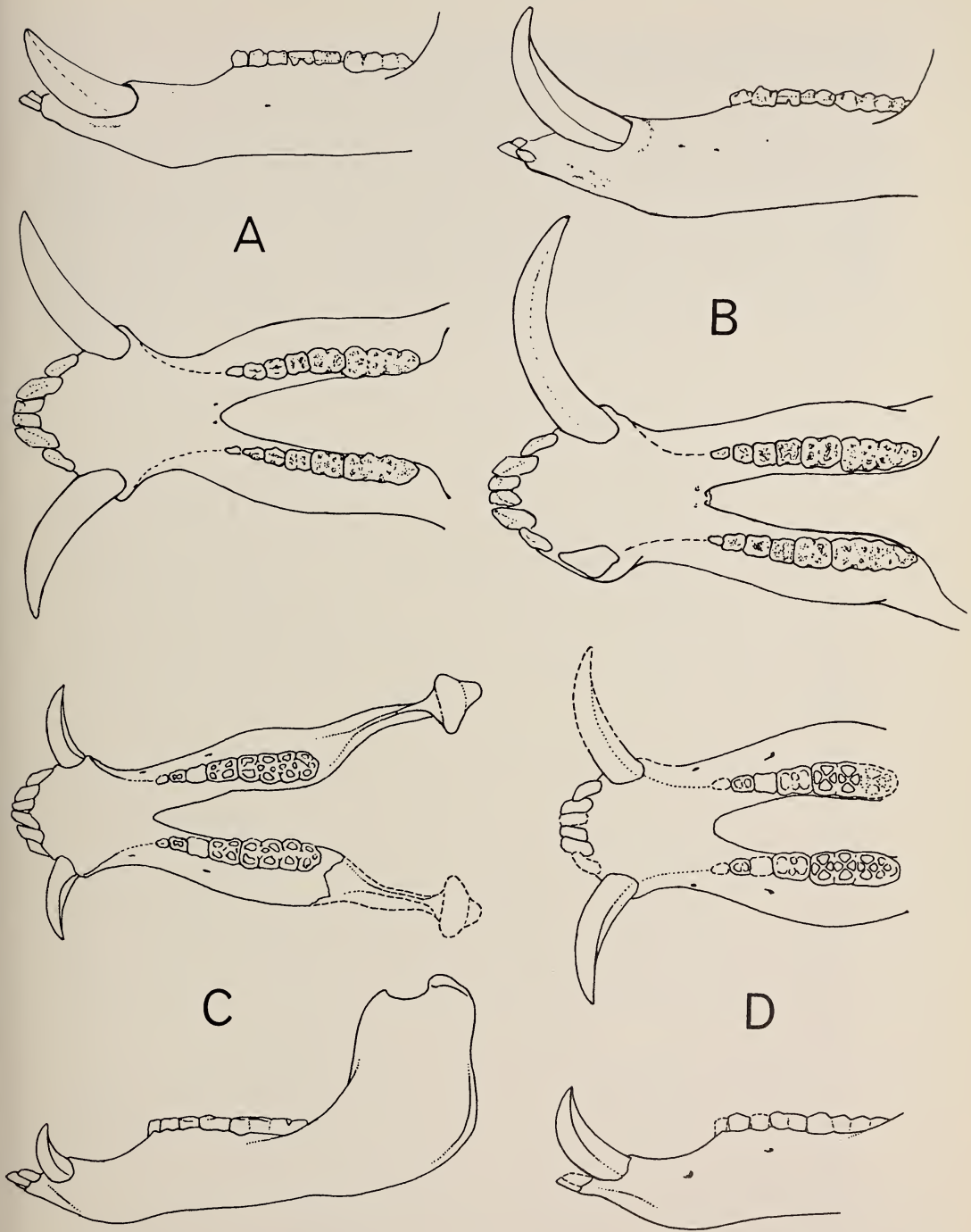


Fig. 7. *Kolpochoerus* mandibles. A. 'Typical' *Kolpochoerus limnetes* (Omo L64-5 and incisors of L36-27). B. 'Advanced' *Kolpochoerus limnetes* (= *olduvaiensis*) (KNM-ER 1314). C. *Kolpochoerus paiceae* (SAM-PQ2166). D. *Kolpochoerus paiceae* (SAM-PQ-E16675 and E20928).

anterior border of the symphysis is only slightly curved whereas in *K. limnetes* it is more nearly semicircular and thus extends farther in front of the canines. The junction of the two rami lies slightly below the lower surface of the corpus in *K. limnetes* and the symphysis rises gently to the incisor border, almost as a straight line in profile, although there is a very weak shelf supporting the procumbent incisors, much as in *Hylochoerus*.

Compared with 'typical' *Kolpochoerus limnetes*, the Skurwerug mandible has a shorter symphysis, only very slightly longer than the breadth across the canines, but its origin is still about level with the front of the premolars. The distance from the front of the premolars to the back of the canine is also reduced, being very slightly less than the length of the M_3 alone. The anterior border of the symphysis is less arcuate, although not as flattened as in *Hylochoerus*. The profile of the symphysis is rounded, very much as in *Phacochoerus* and, like the latter, the incisors are set in a shelf-like projection. All three pairs of incisors are retained, with I_3 not reduced (as it is in *Hylochoerus*) and the structure of the incisors is basically similar to that in *Sus*, but perhaps closer to that of *Hylochoerus*. The ascending ramus is a little different from the few *K. limnetes* jaws in which it is preserved, for in these specimens the anterior edge is more upright than in PQ2166 and antero-posteriorly narrower, especially in the 'advanced' form (e.g. see Harris & White 1979, pl. 11—KNM-ER 1314). In PQ2166, also, the rear edge of the ascending ramus is farther back from the end of the cheek teeth, giving a 'stretched-out' appearance to the ascending ramus. The height to the condyle is also less than in 'typical' *K. limnetes* and considerably less than in the advanced form. Some measurements covering a substantial time range are given in Table 3.

The lower dentition (Table 2; Figs 2, 8, 9)

The lower canines of PQ2166 emerge from the symphysis almost perpendicular to the axis of the mandible and rise at a low angle, which is typical of *Kolpochoerus limnetes*. They extend 6 to 7 cm from the alveolar border and are very similar to the canines from Olduvai Bed I that are attributed to females, although perhaps a little more robust. The cross-section is subtriangular with a somewhat rounded anterior keel. The posterior facet is 18 mm broad at the alveolar margin, the antero-dorsal facet 21 mm broad and the antero-ventral one 22 mm. The two larger faces are covered with thin enamel that is weakly striated longitudinally. There is a strong wear facet 4–5 cm long on the back of the tooth. There are no anterior wear facets indicative of extensive digging.

The lower premolars of PQ2166 are reduced in size and number compared with the 'typical' East African *K. limnetes*, in which P_2 is almost invariably present although in the 'advanced' form it may be shed in the mature adult. Only in one 'advanced' specimen from Koobi Fora, KNM-ER 6, is P_2 apparently absent and P_3 is slightly reduced in size, but the P_4 is normal.

The P_3 of PQ2166 is a simple double-rooted tooth that is morphologically a stouter version of the upper P^2 . The anterior root is stouter and longer than the



Fig. 8. Occlusal view of the right lower cheek teeth of the *Kolpochoerus paiceae* mandible from Skurwerug (SAM-PQ2166). Natural size.

posterior one, and the anteriorly tapering part of the crown which it supports is correspondingly longer, but narrower, than the posterior section. A single elongated dentine island has been exposed by wear. In *K. limnetes* there is a stout main central cone linked to a well-developed posterior cingulum cone and to a weak anterior cingulum cusp. In PQ2166 the anterior cingulum cusp is lacking.

The P_4 of PQ2166 is a double-rooted tooth that is appreciably larger than P_3 . The P_4 is well worn in both halves of the mandible, and the occlusal surfaces are taken up by figure-of-eight exposures of dentine, flanked anteriorly by a prominent cingulum. The characteristic offset of the double central cusp is apparent and the pattern is normal for *Kolpochoerus limnetes*, though the crown tapers a little anteriorly as compared with the usual rather rectangular crown. The reduction in size of P_3 and P_4 in comparison with the sample from Olduvai Bed I is clear from Figure 9.

Both left and right M_1 of PQ2166 are well worn, the only enamel remaining being on the lingual surfaces of these teeth. They evidently had paired cusps anteriorly and posteriorly, the latter being slightly the broader.

The left and right M_2 are also heavily worn, but sufficient enamel remains on the occlusal surface to show that the cusps consist of anterior and posterior pairs, separated by the two median cusps, and flanked by anterior and posterior cingula. The M_1 and M_2 are at the low end of the size range for the Olduvai Bed I sample but are otherwise unremarkable (Fig. 9).

In the M_3 of PQ2166, the trigonid and talonid are of similar size and, except for the anterior cingulum of the trigonid, they are nearly replicas of one another. Except for its slightly larger size and absence of a posterior cingulum, the M_3 trigonid is similar to M_2 , with paired cusps anteriorly and posteriorly separated by two median cusps, with two other median cusps anteriorly and posteriorly. This paired cross-shaped cluster of four cusps is also the pattern of the talonid, although there is an additional small cusp developed postero-lingually on the

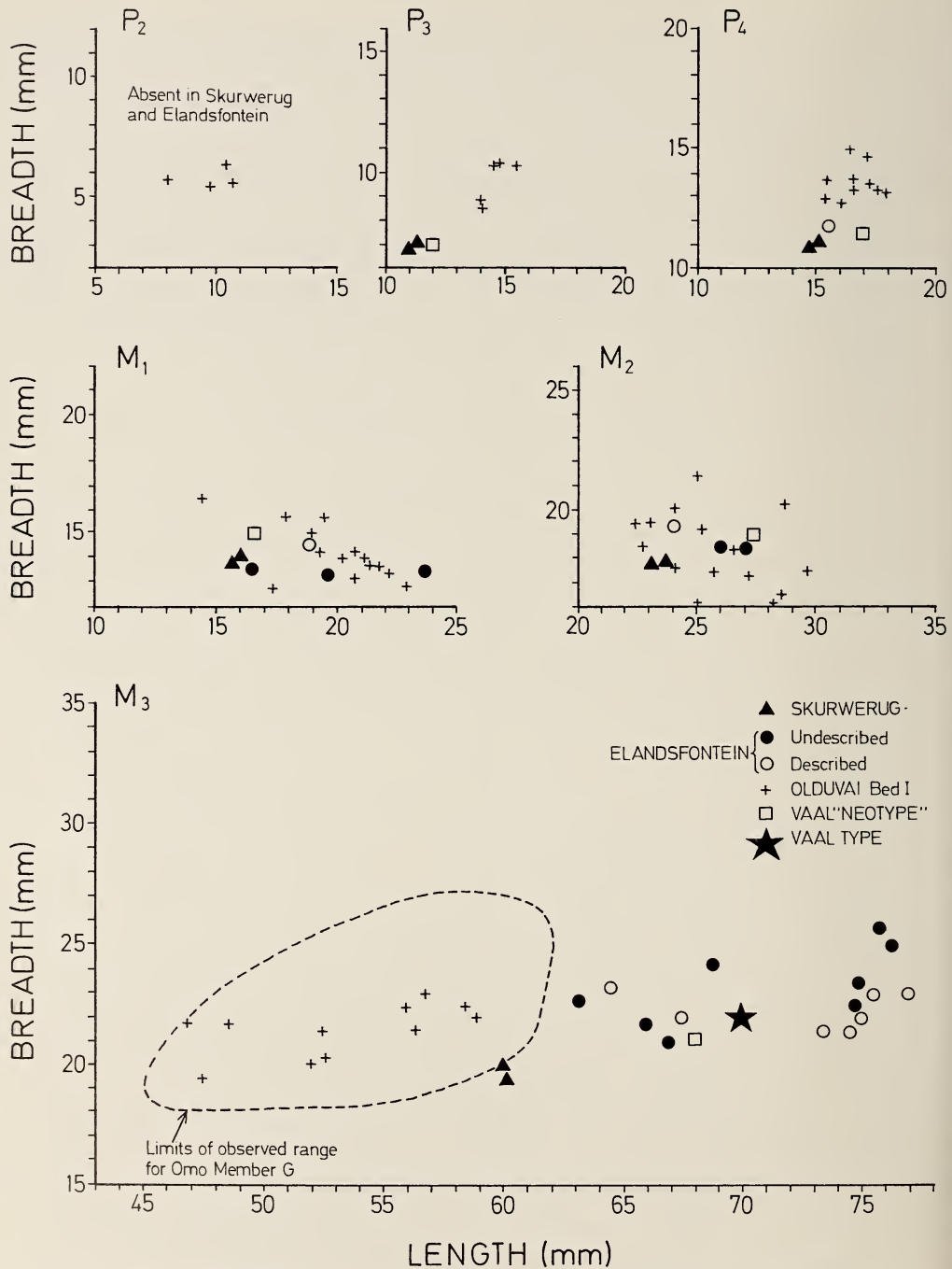


Fig. 9. Length/breadth measurements of lower cheek teeth of *Kolpochoerus paiceae* from Skurwerug, Elandsfontein and the Vaal River gravels, *K. limnetes* from Olduvai Bed I, and an advanced *Kolpochoerus* from Peninj.

most posterior median cusp. The presence of four pairs of laterals is a moderately advanced characteristic and the M_3 lies at or just above the upper limit for the Olduvai Bed I sample (Fig. 9). The crown height is not abnormal for teeth at this stage in the lineage.

THE ELANDSFONTEIN MATERIAL

Figs 7D, 10–14

Singer & Keen (1955) described a small collection of suid remains from the farm Elandsfontein, the locality from which the 'Saldanha' hominid skull had been recovered (Drennan 1953); the site is often referred to in the literature as 'Hopefield'. The material consisted of jaw fragments and teeth apparently representing the remains of 12 individuals. Comparisons were made with the then known material of *Mesochoerus olduvaiensis* and a new species was created, *M. lategani*, with the type consisting of seven fragments comprising an incomplete set of upper and lower cheek teeth of a single animal. Keen & Singer (1956) added descriptions of four more third molars referred to *M. lategani* and also a mandibular fragment with RM_3 (ES28), which they referred to *M. paiceae*; they also removed the previously described M_3 (ES21) and referred it to *M. paiceae*. A left mandibular fragment with an unworn M_1 , D_4 and part of D_3 was referred to *Mesochoerus* but not named specifically. The 1956 collection also included the upper second and third molars (ES26) of a much larger suid referred to what was then called *Tapinochoerus meadowsi* but Harris & White (1979) refer it to *Metridiochoerus compactus* (= *Stylochoerus compactus* of Cooke & Wilkinson 1978). Three additional incomplete third molars (E9171, 11765 and 12040) have since been recovered and serve to confirm this identification. The age of the bulk of the Elandsfontein fauna is assessed as approximately coeval with the upper part of the Olduvai succession (Bed III or IV), but it also includes younger elements, and some material may even be older (Hendey 1974).

Subsequent to these accounts, additional material referable to *Kolpochoerus* has been recovered, mostly pieces of maxilla or mandible with two or three cheek teeth, and a few isolated molars and canines. The most complete specimens are two partial maxillae of one individual with RP^3 – M^3 and LP^4 – M^3 (E16550A, B) and two rather damaged mandibles (E16675 and E20928), which include the symphyseal areas. Measurements on all the teeth are plotted in Figures 5 and 9, with the described and undescribed material distinguished by open and solid circles respectively. Although few of the premolars are preserved intact, the roots or sockets are present on several specimens and demonstrate the same reduction in numbers and size as are displayed by the Skurwerug skull.

No upper incisors are known in the Elandsfontein collection but there are three upper canines—a pair E16297 (Fig. 10) and a poorly preserved specimen E11808. These specimens are appreciably stouter than the upper canines of the Skurwerug cranium; they are considerably shorter than normal males of *K. limnetes* but they probably do belong to male animals as they are too big to be



Fig. 10. Ventral and dorsal views of left and right upper canines respectively of *Kolpochoerus paiceae* from Elandsfontein (SAM-PQ-E16297).

female. Nevertheless, they are very different from the strongly flared hylochoerine to phacochoerine ones of 'advanced' *Kolpochoerus* (e.g. KNM-ER 788 in Harris & White 1979, pl. 9) and, as the Elandsfontein deposit is almost certainly coeval with very advanced *Kolpochoerus* in Olduvai Beds III and IV, this is regarded as a significant feature of *K. paiceae*.

The P³ is known only by the posterior root in the maxilla of E16550A (Fig. 11). The entire tooth is estimated to have been about 13 mm long and 11 mm wide, or very slightly larger than in the Skurwerug cranium. The P⁴ is also present in this specimen and its mate in E16550B. They are also slightly larger than in PQ2166 but are structurally similar in having a molariform aspect. There is an



Fig. 11. Lingual and occlusal views of the right upper cheek teeth of *Kolpochoerus paiceae* from Elandsfontein (SAM-PQ-E16550).

anterior cingulum made up of four small cusps, paired cusps anteriorly and posteriorly that are separated by a small median cusp, and a reduced posterior cingulum made up of two small cusps. The process of molarization is not carried quite as far as in *Hylochoerus* but the trend is similar. The only other P⁴ is in a maxilla fragment (ES7) but in this specimen the configuration is more normal for *Kolpochoerus* with two buccal cusps, one lingual cusp, and anterior and posterior cingula that are made up of several smaller cusps (Singer & Keen 1955, pl. 23D). The enamel of the principal cusps is more crenulated than in the P⁴ of PQ2166.

The upper first molar is preserved in E16550A (Fig. 11) but is broken away in its mate. Although the fundamental pillar structure is normal, the tooth is worn to the point at which large areas of dentine are exposed, together with ribbons and rings of enamel; the M³ in this specimen is still incompletely erupted with only the

front pillars in wear, so the extent of the wear on M^1 is a little surprising. M^1 is also present in ES7 in which the wear is a little less advanced and the structure is normal (Singer & Keen 1955, pl. 23D).

There are five examples of M^2 , in various stages of wear, and they are essentially similar to the teeth of 'typical' *K. limnetes*. The enamel of the principal cusps is more crenulated than in PQ2166 and there is a heavier covering of cement, both of which Harris & White (1979) regard as progressive characteristics. Another specimen, E2647/8, has the M^1 and M^2 worn at an unusual angle, apparently due to abnormality in eruption.

There are 17 examples of M^3 , some of them incomplete but 12 are measurable and represent at least 10 individuals. Length/breadth plots are given in Figure 5. The teeth are all larger than the M^3 of the Skurwerug cranium, carry a heavier coating of cement, and are relatively higher crowned. Most of the specimens have three pairs of lateral pillars with a terminal complex that may include an incipient fourth pair of laterals. One of the smaller specimens, ES23 (Keen & Singer 1956, pl. 33A) is unusual in having a total of only four pillars on the talonid, namely a small median, the third pair of laterals, and a stout terminal pillar. The smallest tooth, ES24, has the same arrangement of pillars as in the Skurwerug cranium, although the crown is 6 mm longer. The third molars in the pair of maxillae, ES16550, are similar in size to ES23 and ES24 yet have four fully developed pairs of laterals and a pair of terminal pillars of smaller size (Fig. 11). The unworn third pair of laterals have a height of 36 mm. The largest teeth are a pair, ES14 and ES15, in which the fourth pair of lateral pillars is quite well developed, plus a small double terminal pillar (Singer & Keen 1955, pl. 21A). ES15 reaches a crown height of 42 mm on the unworn second lateral pillars. In contrast, ES27 is equally large yet has only three pairs of laterals and a terminal complex of smaller pillars (Keen & Singer 1956, pl. 33D). There is thus a good deal of variation within the Elandsfontein sample, more so than in samples from limited time zones in East Africa, perhaps because the former is temporally heterogeneous.

Although there are a number of fragments of the lower jaw, there are only two specimens that demonstrate the morphology. E16675 has the entire symphysis preserved, with some damage to the incisor area, but retaining parts of both canines (Fig. 12). The right ramus is lacking but the left ramus is preserved as far back as the contact with the front of M_3 . Unfortunately the cheek teeth were lost post mortem but the root sockets allow some inferences to be made. P_2 was clearly absent, the roots of P_3 are very small and P_3 and P_4 together occupied a total of 25 mm, while the roots of M_1 and M_2 have a combined length of about 49 mm. The symphysis is slightly longer than in the Skurwerug mandible, and the breadths across the canine flanges and across the post-canine constriction are also greater in E16675 (Table 3). The back of the symphysis lies a little in front of the P_3 . The cross-section of the canines is about the same size as in PQ2166 but they appear to have been considerably longer. It seems likely that the jaw is either that of a young male or, more probably, of a female more robust than PQ2166. The



Fig. 12. Dorsal view of *Kolpochoerus paiceae* mandible from Elandsfontein (SAM-PQ-E16675).

second mandible, E20928, was shattered and the relative positions of the two horizontal rami are slightly distorted in the reconstructed specimen, but it is clear that it was very similar to E16675 (Fig. 13). The canines are appreciably larger and it is virtually certain that this was a male animal. In the two specimens the symphysis is identical in length and a reliable estimate of the breadth across the canines in E20928 is slightly more than in E16675. The back of the symphysis is in the same relative position and both have a curved profile to the symphysis with a projecting shelf for the incisors. The gentle curve of the anterior border of the symphysis is the same but E20928 retains LI_1 , LI_2 , RI_2 and RI_3 . Parts of both canines are preserved. In this specimen, LM_3 is intact, but only the trigonid of RM_3 remains. The rest of the tooth-bearing parts of the corpora are broken, but LP_4 and LM_2 , and RP_4 , RM_1 , and RM_2 have been restored to the specimen. The diastema in PQ2166 is shorter than those of the two Elandsfontein specimens, of which E20928 is the shorter, apparently because of its relatively large canine. The reconstruction of E20928 shows that the sum of the length of P_3 to M_2 was about the same as that in E16675 and in PQ2166. As the horizontal rami and the M_1 and M_2 are larger in the Elandsfontein specimens than in PQ2166, the implication is that the reduction of the premolars was even greater.

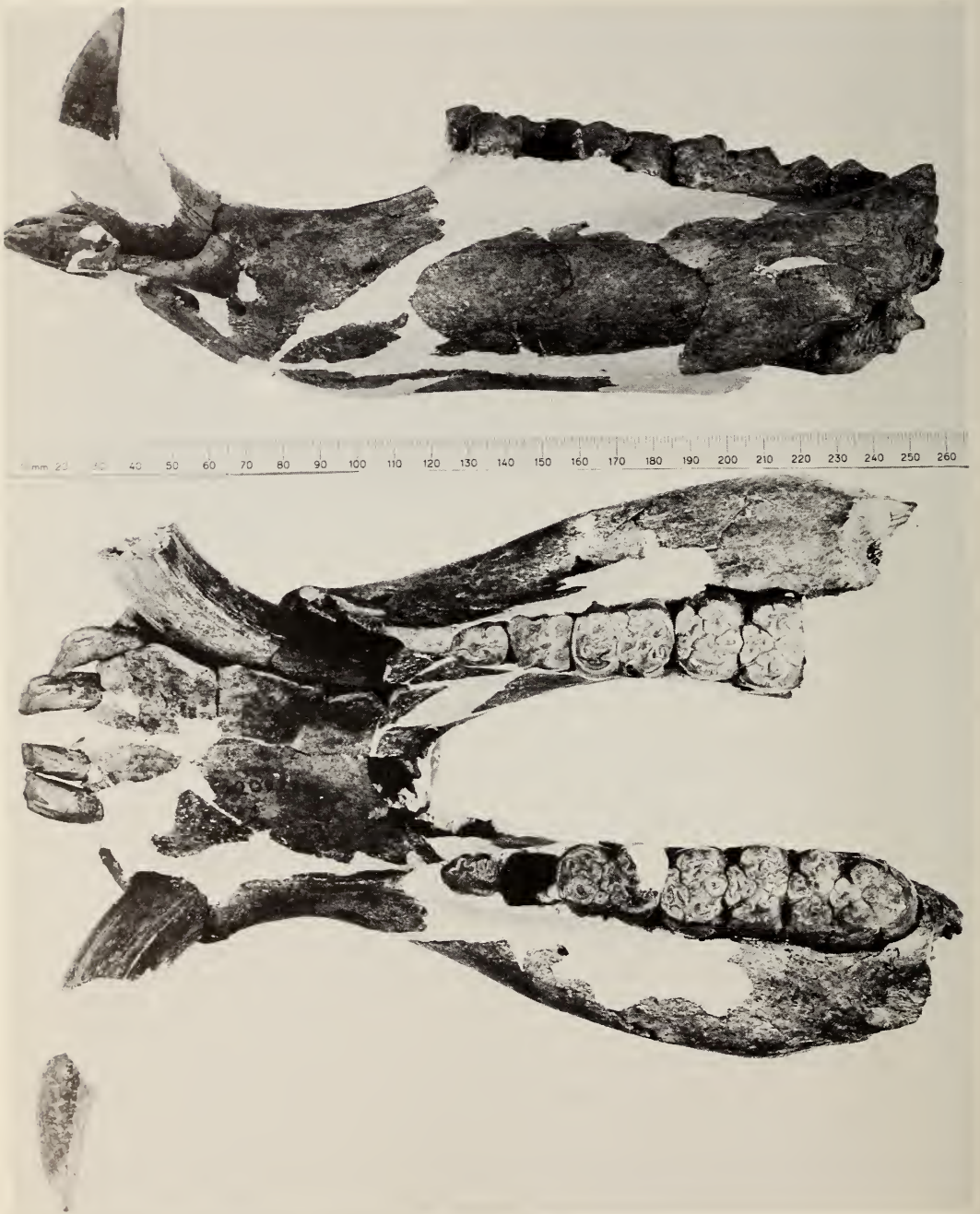


Fig. 13. Lateral and dorsal views of *Kolpochoerus paiceae* mandible from Elandsfontein (SAM-PQ-E20928).

The incisors are known only from the mandible E20928. They are essentially like those of the Skurwerug mandible although the RI_3 is a little wider.

The lower canines occur in the two symphyses, E16675 and 20928, although they are broken above the alveolar margin. In E16675 they are very similar in diameter to those in the Skurwerug mandible but they were clearly longer as the whole of the worn part of the tip is broken away and the remainder is more than 6 cm in length. In cross-section, they are almost heart-shaped or U-shaped, with a broad groove on the posterior face; this shape has been noted in female canines from Bed I, Olduvai. The roots are open but the pulp cavity is small, and the enamel is thin. In E20928 the cross-section is subtriangular with a faint keel caused by a shallow groove on the lateral (lingual) face. The lateral face has a length of 27 mm, the medial face 25 mm and the posterior 20,5 mm, as compared with 22, 21 and 18 mm respectively in the Skurwerug mandible and 21, 21 and 16 mm in E16675. There is no posterior groove and the roots are open in the normal fashion. The left canine of E20928 has been reconstructed and it extends about 10 cm from the alveolar margin, with a root length of at least 8 cm (Fig. 13). It is therefore appreciably longer than the canines of PQ2166, but much shorter than the canines of advanced *K. limnetes* males from East Africa. There are also two other specimens of the lower canine, E4019 and E7949. E4019 is part of a symphysis with 9 cm of the root area preserved; it is essentially similar to E20928. E7949 has lost the root area but the tip is preserved intact and shows a small anterior wear facet; the length is 14 cm as preserved and the cross-section resembles E20928.

In the only three specimens in which the relevant area is preserved, there is no sign of the possible presence of P_2 or of any scar to suggest its existence. Small roots for P_3 are seen in the symphysis E16675 and there is a P_3 socket in one of the specimens (ES17) described and figured by Singer & Keen (1955, pl. 22E, F). Judging from the alveolus, P_3 was even more reduced than that of PQ2166. The posterior root is very compressed, and its alveolus merges with that of P_4 . In addition to an apparent absolute size reduction in the ES17 P_3 compared with that of PQ2166, there is an even greater relative size difference, given the fact that ES17 represents a larger individual, with a molar row length of 123 mm against the 100 mm in PQ2166. Much the same applies in the case of E20928 since, although neither the P_3 nor its alveoli are preserved in this specimen, it is clear from the reconstruction that this tooth was as reduced as that of ES17 (Fig. 13).

The P_4 in the mandible fragment ES17 is slightly broken but the length is estimated as 15,5 mm and the breadth is 11,7 mm, fractionally larger than in PQ2166. There is a strong broad main pillar and a small posterior cusp, as in the Skurwerug jaw. The enamel is somewhat rugose. The best-preserved specimens in the Elandsfontein assemblage are an unequally worn pair associated with the mandible, E20928 (Fig. 13). The more worn right P_4 is morphologically very similar to those of PQ2166 but is slightly smaller. This is a further indication of the relatively greater reduction of the premolars in the Elandsfontein *K. paiceae*, since the mandible of E20928 is considerably more robust than that of PQ2166

(Table 3) and its M_3 is appreciably larger. The P_4 of E20928 is also distinct in having markedly rugose enamel, which is said by Harris & White (1979) to be an advanced character in East African *K. limnetes*.

There are five examples of M_1 . These teeth in E20928 and ES17 are in advanced wear (Fig. 13; Singer & Keen 1955, pl. 22E, F). In the latter the anterior and posterior pairs of pillars respectively are united into enamel-rimmed areas of dentine within which are small residual lakes of enamel; it is larger than the corresponding tooth in PQ2166. The LM_1 is present and unworn in the juvenile jaw fragment ES22 described and figured by Keen & Singer (1956, pl. 34) and in the original 'type' specimen ES5/6 (Singer & Keen 1955, pls 20, 21). M_1 is also present in two undescribed juveniles E5294 and E11859. The last named is also very similar in size to the teeth in PQ2166 but the other two are somewhat larger (Fig. 9). The morphology is normal.



Fig. 14. Occlusal views of the smallest and largest lower third molars of *Kolpochoerus paiceae* from Elandsfontein (SAM-PQ-E3032 and E11680).

M₂ is present in ES17, ES3 and ES6 (Singer & Keen 1955, pls 20, 21, 22) and also, though damaged, in the two fragments of a mandible E11680 and in three other specimens, E20928 (Fig. 13), E20867 and E16910. ES3 is close in size to PQ2166 while the others are somewhat larger (Fig. 9). The morphology is normal for *Kolpochoerus*.

The lower M₃ is well represented in the Elandsfontein assemblage by 14 complete specimens belonging to 12 individuals as well as by several incomplete specimens. Half of these were described by Singer & Keen (1955) or by Keen & Singer (1956). The crown normally consists of four well-developed pairs of lateral pillars with a fifth pair weakly developed at or near the back of the crown. The two largest teeth, E11680A, B (Fig. 14), however, have only four paired laterals and two small terminal pillars that can hardly be termed a fifth pair. Most closely comparable with PQ2166 is the specimen ES28 (Keen & Singer 1956, pl. 33E). It was the only one to be selected by Keen & Singer (1956) for differentiation from '*Mesochoerus lategani*' and placement in Broom's (1931) species '*M. paiceae*'. ES28 is indeed very similar to the M₃ of the type and of the 'neotype' from the Vaal River gravels (Shaw & Cooke 1941), although a little smaller. Both it and the smallest of the Elandsfontein third molars, E3032 (Fig. 14), are a little larger than the corresponding teeth in PQ2166 but are alike in pillar structure. Since the older fossils from Elandsfontein could represent more than one time interval, E3032 and ES28 may belong to an earlier temporal variant of *Kolpochoerus* at this locality. However, in view of the variation in detail in the number and arrangement of the minor elements at the back of the talonid that is normal in *Kolpochoerus* samples, the Elandsfontein sample can be regarded as a single species, so that '*M. lategani*' is a junior synonym of *K. paiceae*. The tallest unworn pillar (in E12822/11445) is 36 mm and it is the same in ES6 and ES16 (Singer & Keen 1955, pl. 20B). Thus the crown height of both upper and lower molars is generally greater than in most specimens from the upper parts of the Shungura and the Koobi Fora formations.

THE ZULULAND SPECIMEN

Fig. 15

During 1976, M. J. McCarthy of the University of Natal collected some fossils, including an incomplete *Kolpochoerus* tooth, from the Port Durnford Formation at Gabhagabha on the Zululand coast (McCarthy & Orr 1978).

This *Kolpochoerus* specimen (SAM-PQ2174) is a left M₃ in an early state of wear that lacks most of the anterior half of the trigonid (Fig. 15). The remaining part of the trigonid is similar in all observable respects to corresponding parts of the M₃ of PQ2166. The talonid also resembles that of PQ2166, as well as the smaller of the specimens from Elandsfontein. It is distinct in having a double median cusp anteriorly, a feature not observed in any other *K. paiceae* specimen. This is probably an individual or population characteristic that has no taxonomic significance. The talonid of PQ2174 lacks the small postero-lingual cusp present in



Fig. 15. Lateral and occlusal view of the *Kolpochoerus paiceae* lower third molar from the Port Durnford Formation, Zululand (SAM-PQ2174). Natural size.

PQ2166, a feature that accounts for the marginally greater talonid length in the latter (c. 29 mm as against 27 mm in PQ2174). The talonids of the smaller Elandsfontein specimens, and of the *K. paiceae* 'neotype' from the Vaal River gravels, are distinguished from that of PQ2174 principally by their slightly greater crown heights, which suggests that the Zululand specimen is in a more primitive evolutionary state. This specimen may therefore be like the one from Skurwerug in representing a somewhat earlier form of *K. paiceae*. Although the bases for comparison are limited, there is nothing that would preclude the Zululand and Skurwerug *K. paiceae* from being broadly contemporaneous.

DISCUSSION

The close similarity in size and morphology between the type M_3 of *Kolpochoerus paiceae* and the M_3 of the 'neotype', both of which came from the Vaal River gravels, leaves little doubt about their mutual identity. In the 'neotype' both P_3 and P_4 are smaller than in any of the East African material and very close in size to the Skurwerug specimen. The 'neotype' has a small pit in front of the P_3 that was interpreted as a root impression for P_2 , but as the M_3 in this specimen is not yet erupted, it is very possible that the anterior premolar would be shed in the adult. The M_3 in the Elandsfontein material covers a size range that includes both the type and the 'neotype' and this, coupled with the unusual reduction in the premolars, provides a sound basis for considering that all

represent the same species. The Skurwerug and Zululand specimens are distinct in having the M_3 slightly smaller than those in the other samples, but they are also identified with *K. paiceae*.

The Skurwerug skull is a good deal smaller than the 'advanced' female cranium from Peninj, although there are general resemblances, as may be expected in females of *Kolpochoerus*. In the Peninj cranium the occipital condyles are elevated well above the palatal plane but this is achieved by elevation of the whole occiput and braincase, as well as by increase of the height of the occiput itself as compared with 'typical' *K. limnetes*. In the Skurwerug cranium the condyles are also higher above the palatal plane than in 'typical' *K. limnetes*, but the occiput itself is shorter and the net result is that the braincase and orbits are not as elevated, although they may be higher than in the 'typical' form. Unfortunately, the braincase and occiput are not known in the best female cranium, KNM-ER 1085 from Koobi Fora, but in that specimen the rim of the orbit is lower than in the Skurwerug cranium. The reduction in size of the occiput in the Skurwerug cranium is unexpected and it is also notable that the paramastoid processes are not very robust. *Hylochoerus* also has elevated condyles and a short occiput but a different occipital morphology. Another point of difference between the Skurwerug cranium and that of the Koobi Fora female KNM-ER 1085 is that, far from the premolar reduction seen in PQ2166, the Koobi Fora female not only had normal-sized premolars but actually retained the P^1 18 mm in front of P^2 . The Peninj female on the other hand had lost P^2 but P^3 and P^4 were larger than normal. The Peninj female had kept the full complement of upper incisors as compared with the reduced complement in PQ2166. Thus the Skurwerug cranium shows a number of important features of difference from both the 'typical' and the 'advanced' *Kolpochoerus* of East Africa.

The two partial mandibles from Elandsfontein, E16675 and E20928, probably represent female and male individuals respectively, and they make it possible to reconstruct the mandible of 'typical' *K. paiceae* with some assurance. By comparison with mandibles of males of 'typical' *K. limnetes* from the Shungura Formation or the Koobi Fora Formation there are several striking features of difference. The corpus is unusually robust and expanded lateral to the second and third molars so that the overall width across the two horizontal rami is much greater than the width at the canine alveoli. The symphysis is unusually short, thus adding to the massive appearance of the jaw. The anterior border of the symphysis is flattened rather than arcuate, emphasizing the relative shortening and broadening of the jaw. The distance from the back of the canine to the front of the anterior premolar is about normal for *K. limnetes*, so the shortening is largely in the anterior part of the symphysis. The canines are stout but are more laterally directed and shorter than in 'typical' *K. limnetes*. While these features, apart from the premolar reduction, might be less striking in specimens from the lower part of the Shungura Formation (i.e. more than 2 Ma), they are very remarkable in the context of an age equivalent to the upper part of the Olduvai Beds (i.e. less than 1 Ma). The evolutionary trend in the 'advanced' *Kol-*

pochoerus from such levels is towards elongation of the jaw, especially of the symphysis, so that the distance from canine to anterior premolar is increased, as well as by forward arching of the incisor border. There is also a trend towards increased curvature and elongation of the canines. There is thus good reason to maintain the separateness of *K. paiceae*.

The Skurwerug mandible is less robust than the Elandsfontein specimens but the width across the two horizontal rami is substantially greater than the width across the canines. The symphysis is short and the incisive border flattened, as in the Elandsfontein material, and the somewhat phacochoerine profile of the symphysis is similar. Considered together with the premolar reduction, these features leave little doubt that the jaw belongs to the same species as the Elandsfontein material.

The lesser robustness of the Skurwerug mandible is consistent with the specimen representing a female, but the difference is greater than might be expected in a contemporary population, an opinion that would be confirmed if E16675 does indeed belong to a 'typical' *K. paiceae* female. It seems likely that the Skurwerug specimen represents an earlier, somewhat less specialized stock. This is borne out by the smaller size of the third molars, for in suids there is normally very little size difference in the cheek teeth of the two sexes. The upper third molars are very slightly larger than those in the Koobi Fora female KNM-ER 1085 which, however, have only three well-developed pairs of laterals whereas PQ2166 has an incipient fourth pair. The third molars from Olduvai Bed I and from the Shungura Member G likewise have three pairs of laterals in the uppers and four in the lowers, although additional posterior small pillars can occur. In size the third molars of the Skurwerug specimen are closely comparable with those from Member G of the Shungura Formation and with the sample from Bed I at Olduvai, both with ages close to 2 Ma. It would seem likely that *K. paiceae* diverged from a stock essentially at the 2-2,5 Ma level of development, strengthening rather than lengthening the talon (taloid) of the third molars while concurrently reducing the premolars and the upper incisors, molarizing the P⁴, shortening the symphysis, and increasing the robustness of the mandibular corpus, raising the level of the occipital condyles and reducing the height of the occiput itself. It seems reasonable to suggest that the Skurwerug skull retains more *K. limnetes*-like morphology than would be apparent in the later Elandsfontein sample, although the Skurwerug specimen is already clearly differentiated from its parent stock. It is therefore likely to date back between 1 and 2 Ma, and it seems desirable to allow about 0,5 million years for the continued specialization represented by the material from Elandsfontein. The bulk of the fossils from Elandsfontein have an age estimated as about 0,8 Ma (\pm 0,2 Ma) on the basis of correlation with Olduvai Beds III/IV.

Although not necessarily associated with PQ2166, the other fossils from Skurwerug are not inconsistent with this age estimate. The *Gazella* sp. is of some significance in suggesting a middle Pleistocene or older date, since this genus has not been recorded in younger faunas from the south-western Cape Province.

PALAEOENVIRONMENTAL IMPLICATIONS

Apart from its significance in terms of the history of the genus in South Africa, the Skurwerug *Kolpochoerus* specimen is remarkable in several other respects. Firstly, Suidae are a rare element in the Pleistocene faunas of the southwestern Cape, and they were not present in this region at all during historic times. Even the large and diverse fossil assemblage from Elandsfontein includes relatively few suid specimens, with no more than a dozen *Kolpochoerus paiceae* and even fewer *Stylochoerus compactus* individuals having been recorded on the basis of very incomplete material. PQ2166 therefore stands out amongst the approximately 30 fragmentary fossils that make up the mammalian assemblage from Skurwerug. However, judging from other fossil occurrences in the vicinity of Saldanha Bay, it is likely that immense numbers of specimens were preserved in the Skurwerug dune, and it was only the scale and nature of the excavation and the restricted access to the site that prevented a more representative sample being collected. Thus, it is possible that the Skurwerug *K. paiceae* was as common an element in the fauna of its time as its counterpart from Elandsfontein.

The recovery of PQ2166 was clearly fortuitous, and was almost certainly due to the relatively large size and completeness of the specimen, which no doubt made it an obvious curiosity to the persons involved in its discovery and subsequent donation to the South African Museum. Indeed, it is the condition of the specimen that is perhaps its most remarkable feature. It is unquestionably the most complete suid specimen yet found in the Pleistocene deposits of the southwestern Cape, and one of the best-preserved skulls of *Kolpochoerus* known anywhere. Many of the parts that are missing were lost after it had been excavated, and apparently only the left ascending ramus of the mandible was not preserved at all. The adjacent part of the left mandibular corpus shows signs of weathering on its lateral surface, suggesting that this area and the missing ascending ramus remained exposed after the rest of the skull had been rapidly buried and so preserved intact. Rapid burial was evidently the exception rather than the rule amongst recorded Pleistocene mammal fossils of the region. A high proportion of these specimens show signs of post-mortem damage caused by weathering and the activities of predators, scavengers and bone-gnawing animals such as the porcupine.

Since there is no record of the relationship between PQ2166 and the deposits in which it was incorporated, the taphonomy of this specimen cannot be determined with certainty. However, since the deposits represent a coastal dune, it is likely that the rapid burial of the specimen was effected by wind-blown sand. An implication of this is that the Skurwerug dune was still active at that time, and that PQ2166 therefore gives a direct indication of the age of the dune (i.e. early Pleistocene). It is, of course, also possible that the specimen became incorporated in the deposits after the dune had been stabilized through consolidation and a covering of vegetation. Solution cavities and small caves or burrows excavated by animals are features of consolidated calcareous dunes, and PQ2166 may have been deposited in such a feature. This could have resulted from the death of the

animal that had sheltered in such a cave or burrow, or as a result of the activities of another cave occupant. The latter alternative is unlikely, since the specimen shows no sign of the damage that characterizes the activities of man, hyaenas and porcupines, the only habitual cave-inhabiting bone-collectors that might have been involved in this instance. Even if PQ2166 does post-date the consolidation of the Skurwerug dune, it need not necessarily be much younger. The consolidation of local late Cenozoic calcareous dunes was often, or invariably, a relatively rapid process, so an early Pleistocene date for the one at Skurwerug could still apply. In spite of all these uncertainties, it is clear that the Skurwerug dune cannot post-date the *Kolpochoerus* specimen.

An early Pleistocene age for this dune is in accord with a recently published view on the relationship between late Cenozoic deposits and sea-level changes in the Saldanha region (Hendey 1981a, 1981b, 1983a). According to this interpretation of available evidence, the succession has not been affected by local tectonism and it reflects the global record of sea-level changes. That part of the record which is relevant here began during the early Pliocene when the sea rose to about 100 m above its present level, creating a channel linking Saldanha Bay to St. Helena Bay, with a large island forming its western margin and the mainland following a series of granite hills to the east (Hendey 1981b, fig. 5). This event represents the eustatic cycle TP1 of Vail *et al.* (1977), and is documented by the Varswater Formation, particularly the exposures in 'E' Quarry near Langebaanweg, where a rich fossil assemblage provides evidence of its age. During the middle and late Pliocene, sea-level fell and during this regressive phase there was a stillstand at about 50 m above present sea-level (cycle TP2). During a late Pliocene high-stand that was at about 20 m above present sea-level (cycle TP3 or Q1*), a 12 m submarine platform was developed at wave-base away from the shoreline in Saldanha Bay. This feature reflects the erosion that occurs in the upper 10–15 m of the marine environment (Flemming 1976). The platform is still visible inland from the north-eastern shore of Saldanha Bay, and is underlain by marine deposits that represent the Uyekraal Shelly Sand Member of the Bredasdorp Formation (Rogers 1983). The fluvial deposits at Baard's Quarry near Langebaanweg are correlated with the 20 m high sea-level. The 12 m platform has evidently remained above sea-level since the regression that followed its formation. The Skurwerug dune is situated on the southern margin of this platform, which it overlies and clearly post-dates (Fig. 16). On the basis of this interpretation of local sea-level history during the late Tertiary, the Skurwerug dune must be of late Pliocene or younger age. The possible correlation of this dune with past sea-level changes may, however, be taken still further.

The actual elevation of the interface between the Skurwerug dune and the 12 m platform is not recorded, but judging from 1:10 000 orthophoto maps of the

*Q1 is a Quaternary cycle according to the definition of this period by Vail *et al.* (1977) and Beard *et al.* (1982), but it falls into the Pliocene if the Plio-Pleistocene boundary is taken at about 1.6 Ma (see Tauxe *et al.* 1983), the date which is accepted here. For the purposes of this study the early-middle Pleistocene boundary is taken at 700 ka and the middle-late Pleistocene boundary at 130 ka (see Butzer 1974).

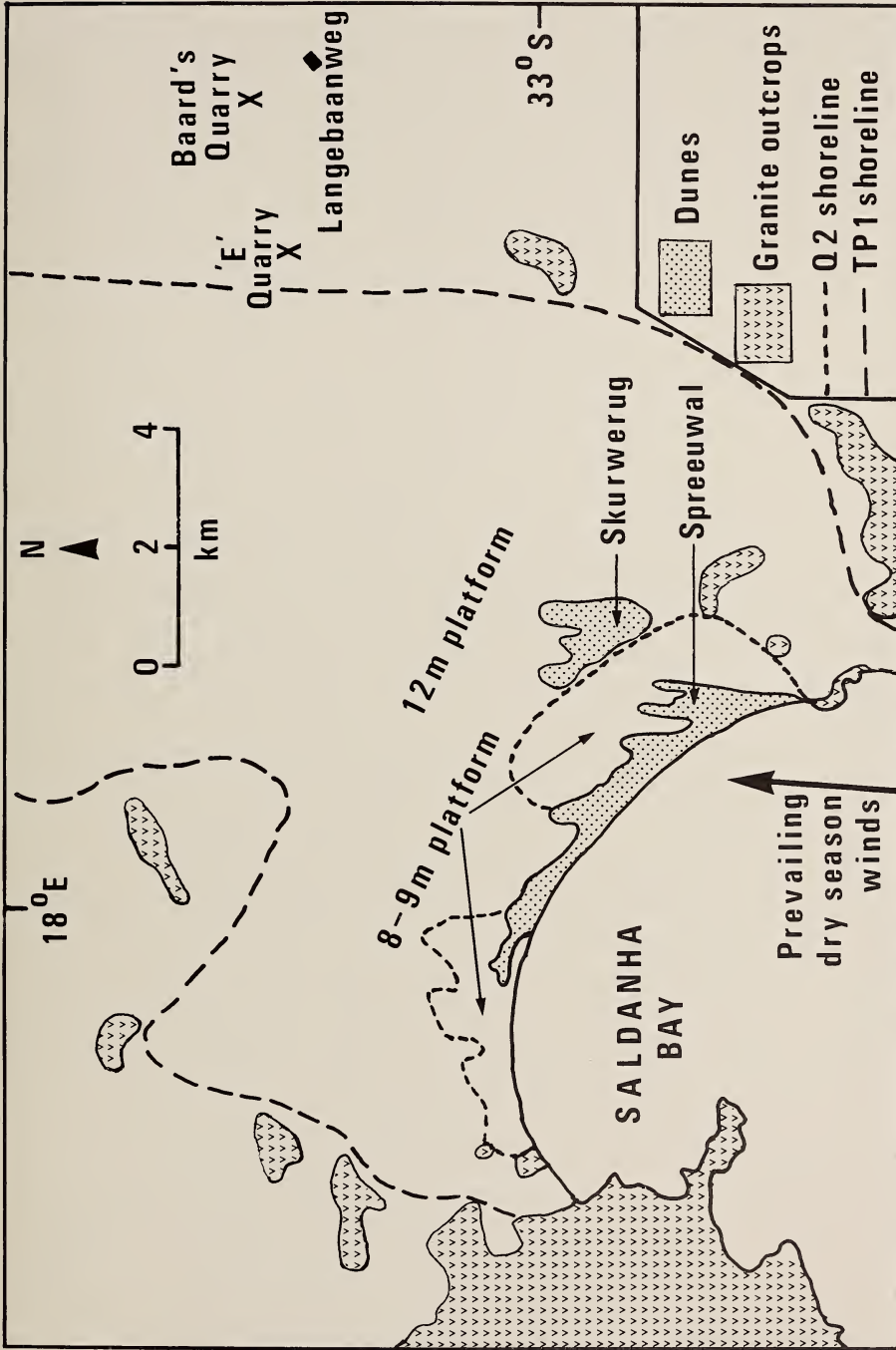


Fig. 16. Sketch-map of part of the Saldanha region showing localities and features referred to in the text. (Adapted from South African Geological Survey map 3217D & 3218C—St. Helena Bay, 3317B & 3318A & 3318A—Saldanha Bay.)

area it must be in the order of 10 to 12 m. Between this dune and the Spreewal dune complex that fringes the present coastline is another platform, this one having an elevation of 8 to 9 m. It is here interpreted as a wave-cut platform that was developed in the intertidal zone during the high sea-level that existed when the Skurwerug dune itself fringed the coastline. Since this dune was situated on the coast and was probably no more than a few metres above sea-level, and since the 8 to 9 m platform has a veneer of aeolian sands, the actual elevation of the high sea-level concerned must have been at or a little below 8 m. There is in fact abundant evidence on the southern African west coast of a past high sea-level at about 7 to 8 m above present sea-level (e.g. Krige 1927; Mabbutt 1957; Hallam 1964; Carrington & Kensley 1969; Tankard 1976; Davies 1980). On the basis of the record of the *Kolpochoerus* specimen in the Skurwerug dune, this high sea-level is now dated as early Pleistocene.

Since this dating conflicts with most previously published opinions on the age of the 7–8 m high sea-level, the situation needs to be reviewed. Perhaps the most widely held opinion is that this high sea-level dates from the last (or Eemian) interglacial. For example, Davies (1980: 165) has stated that the Eem I (= oxygen isotope substage 5e) high sea-level at about 125 ka 'is widely accepted as around + 8 m over much of the world', and he cites local examples suggesting that this was also the case in at least some parts of southern Africa. However, in instances where evidence of age is available, that which indicates an Eemian age is equivocal, while that which indicates a pre-Eemian age is not. The evidence for selected areas or localities around the southern African coast is examined below.

Apart from the Skurwerug evidence, perhaps the most secure indication that the 7–8 m high sea-level on the southern African coast predates the last interglacial comes from the Port Durnford Formation on the Zululand coast (Hobday & Orme 1974). The mammalian fauna from near the base of this formation is clearly pre-Eemian, and is generally regarded as being of middle Pleistocene age (McCarthy & Orr 1978). The Port Durnford Formation *Kolpochoerus* tooth described above could be broadly contemporaneous with the Skurwerug *K. paiceae*, and the formation itself may therefore be earlier than has hitherto been supposed. There is in fact nothing in the Port Durnford fauna that precludes this possibility. The dating of this fauna had been based largely on an elephant, which has been identified as either *Loxodonta atlantica zulu* (Maglio 1973) or *Elephas zulu* (Beden 1983). According to Maglio (1973) it is essentially similar to the middle Pleistocene elephant from Elandsfontein. Elsewhere in Africa *L. atlantica* dates back beyond 2 Ma, so if the identification with this species is correct, then the Zululand elephant could be of pre-middle Pleistocene age. However, it is more likely that the material represents a species of *Elephas*, as indicated by Beden (1983). Since it is clearly less advanced than other middle Pleistocene representatives of this genus in southern Africa (e.g. *E. iolensis* from the Vaal River gravels and Victoria Falls), an early Pleistocene age for this elephant, and for the Port Durnford Formation, is probable.

The decision by Hobday & Orme (1974) to assign an Eemian date to the Port Durnford Formation appears to have been based largely on the artefact associations of this formation, and the mistaken belief that the Acheulian and Sangoan industries persisted well into the late Pleistocene. According to Hobday & Orme (1974), an Acheulian artefact was recovered from this formation, and if this was indeed the case, then it would be further evidence of a pre-Eemian age for the formation, since the Acheulian is no younger than about 150–200 ka anywhere in Africa (Volman 1984). In addition, a so-called 'Sangoan' handaxe was found on the surface of this formation, and although the age of the 'Natal Sangoan' or 'Tugela Industry' (Davies 1980) is not known, it is likely to be pre-Eemian. While there may be doubts about the nature and implications of the archeological associations of the Port Durnford Formation, the faunal evidence is unequivocal in indicating a middle Pleistocene or earlier date for this formation. Judged on both sea-level evidence and the *Kolpochoerus* occurrences, it is very likely that this formation is an east-coast temporal equivalent of the Skurwerug dune.

At the same latitude as the Port Durnford Formation, but on the opposite side of the subcontinent near Oranjemund in South West Africa are deposits associated with a 7–8 m high sea-level that are termed the 'C Beach' or 'Main Terrace' (Hallam 1964: 701). The C Beach, like the Port Durnford Formation, has recently been dated as an Eemian interglacial feature (Anonymous 1982). This dating is unacceptable since Acheulian artefacts have been found overlying the C Beach (Davies 1980; Corvinus 1983). Corvinus (1983) concluded that the archeological evidence indicates an age for this beach of between 400 and 700 ka although this dating is clearly tentative given the nature of the artefact association with the beach and the uncertainties surrounding the chronology of the Acheulian in Africa. Perhaps all that can be safely concluded from this evidence is that the C Beach is middle Pleistocene or older.

There are several records in the south-western and southern Cape Province of Middle Stone Age (MSA) artefacts associated with the 7–8 m high sea-level. Such occurrences have been used to conclude an Eemian interglacial or even younger age for this high sea-level. For example, this applies in the case of the open-air sites at Melkbos (Duinefontein) (Hendey 1968) and Bok Baai (Mabbutt *et al.* 1955), and the cave sites of Die Kelders 1 (Tankard & Schweitzer 1974) and Klasies River Mouth 1 (Butzer 1978). Vertebrate fossils and MSA artefacts were found at Duinefontein (see Fig. 1) in deposits that post-date a 6–8 m high sea-level (Hendey 1968). Although originally assigned to the last glacial period, it is now clear that these materials are much older and pre-date the Eemian interglacial, with the fauna indicating a 'later Middle Pleistocene' age (Klein 1976: 16). Early Stone Age (Acheulian) artefacts are also known from the area (Hendey 1974). The situation at Duinefontein is similar to that at Bok Baai, 12 km further north, where deposits overlying a 6–8 m beach contain both MSA and Acheulian artefacts (Mabbutt *et al.* 1955). In both these instances the 7–8 m high sea-level can be no younger than middle Pleistocene. The same applies at Cape Hangklip

(Fig. 1), where Acheulian artefacts 'extend to within 8 m of present sea-level' (Mabbutt 1957). The caves, Die Kelders 1 and Klasies River Mouth 1, were cut by a high sea-level of about 7–8 m and partly because the earliest recorded human habitation of these caves was during the MSA, this high sea-level was dated as Eemian. However, it was also admitted that in both these instances the caves could have been created before this interglacial, and then scoured by the highest of the Eemian transgressions (Tankard 1975; Butzer 1978).

The Eemian sea-level peak was reached during isotope substage 5e and was probably at about 4–5 m above the present level. This is the elevation of the B Beach at Oranjemund, which is associated with MSA artefacts (Corvinus 1983). Boulder ramparts and other features in the Saldanha Bay–Langebaan Lagoon area that indicate a high sea-level of up to 4,5 m were described by Parker (1968). Flemming (1980) gave a slightly lower estimate (3–4 m) for this high sea-level on the basis of wave erosion features and beach deposits on the Langebaan compound barrier, and suggested a mid-Holocene age for this event. It is here regarded as Eemian in age, although there is a beach ridge on this barrier 1 km east of Kreefbaai with a minimum elevation of 1,5 m (Flemming 1980) that evidently does represent a Holocene high sea-level. There is evidence that indicates that the age of events involved in the development of the Langebaan barrier were generally underestimated in earlier studies (e.g. Parker 1968; Birch 1976; Flemming 1977, 1980). The intertidal-flats deposits near Churchhaven contain vertebrate fossils that are middle Pleistocene or older. These fossils include undescribed elephant teeth that are in the collections of the South African Museum. They represent two extinct species. One is unidentified, but it may belong to a species that is of pre-middle Pleistocene age. The second is *Elephas iolensis*, an elephant that in southern Africa is known only from middle Pleistocene contexts. The deposits from which these specimens were derived overlie the core of the compound barrier, which Flemming (1977, fig. 22; 1980, fig. 51) incorrectly dated as 'late Pleistocene'. Clearly, the barrier can be no younger than middle Pleistocene, and it may in fact be even older. Consequently, the *circa* 4 m high sea-level that is reflected by deposits and features on the barrier need not be as young as Flemming and others have supposed.

The 7–8 m high sea-level has been dated as early Pleistocene on at least one previous occasion. This was done by Tankard (1976) on the basis of the record in the Saldanha region. Unfortunately, he based this dating on an incorrect correlation of the 7–8 m high sea-level in this region with the '45–50 m transgression complex' in Namaqualand, and on the mistaken assumption that the dating of this complex as 'Early Pleistocene' by Carrington & Kensley (1969) was correct. The former error arose from his unsubstantiated belief that the south-western Cape coast has been down-warped relative to that in Namaqualand, an opinion that was discounted by Hendey (1981a). A major objection to Tankard's (1976) correlation is that the 7–8 m high sea-level in the south-western Cape is associated with a cold-water molluscan fauna, whereas the fauna associated with the 45–50 m complex in Namaqualand includes warm-water elements. Tankard

explained this inconsistency by postulating lower sea temperatures in the Saldanha area. In fact, sea temperatures in the relatively shallow and enclosed Saldanha Bay are higher than those on the open Namaqualand coast, and there is no reason to suppose that the situation differed during the early Pleistocene. Although the basis for Tankard's dating of the 7–8 m high sea-level in the Saldanha region is unacceptable, it is perhaps significant that he recognized it to be of pre-Eemian age.

Another succession in the south-western Cape that has been correlated with the 7–8 m high sea-level is that at Swartklip on the False Bay coast (see Fig. 1). Barwis & Tankard (1983) have assigned an Eemian age to the Swartklip succession largely by inference. The only dateable element in this succession is a vertebrate fossil occurrence, which is probably of early last glacial age (Klein 1975). Since the fossils were accumulated in a small cave that was developed after consolidation of the deposits, they clearly post-date the sea-level events that led to the development of the Swartklip succession. The dating by Barwis & Tankard (1983) depended upon their acceptance of a late Pleistocene date for similar successions elsewhere on the South African coast, and their belief that these successions are contemporaneous with that at Swartklip. The other successions include the Port Durnford Formation, which was shown above to be of pre-late Pleistocene age. Presumably, its correlation with the Swartklip succession still applies, in which case the latter is also likely to be a temporal equivalent of the Skurwerug dune. A pre-Eemian date for the Swartklip succession also follows if it is accepted that the Spreeuwal and other dune plumes of the Cape west coast had their origins during the Eemian interglacial (see below). These plumes, which in part represent the Witsand Member of the Bredasdorp Formation, are younger than the consolidated deposits of the Swartklip succession and the Skurwerug dune, both of which are included in the Langebaan Limestone Member of this formation (Rogers 1983).

Two important points emerge from the preceding discussion. Firstly, since the late Cenozoic shorelines of the Saldanha region are unaffected by local tectonism, and since the 7–8 m shoreline is virtually ubiquitous on the southern African coast, it follows that this shoreline reflects a eustatic sea-level event. Secondly, this event represents a high sea-level stand that followed the one that peaked at about 20 m. The latter high sea-level has previously been dated as late Pliocene, with the opinion that it is more likely to date from the eustatic cycle Q1 than cycle TP3 (Hendey 1981*b*). If this is indeed the case, then the 7–8 m high sea-level is most likely to date from the subsequent cycle, Q2. According to Beard *et al.* (1982, fig. 1), the Q2 high sea-level stand occurred between 0,80 and 1,3 Ma, dates that are not inconsistent with the 1–2 Ma age estimate suggested for the Skurwerug *Kolpochoerus* on the basis of its evolutionary development. This fossil therefore dates from the latter part of the early Pleistocene, according to the subdivisions of this epoch accepted here (see footnote p. 44). The sea-level changes indicated by features and deposits in the Saldanha region are illustrated in Figure 17, and are summarized in Table 4.

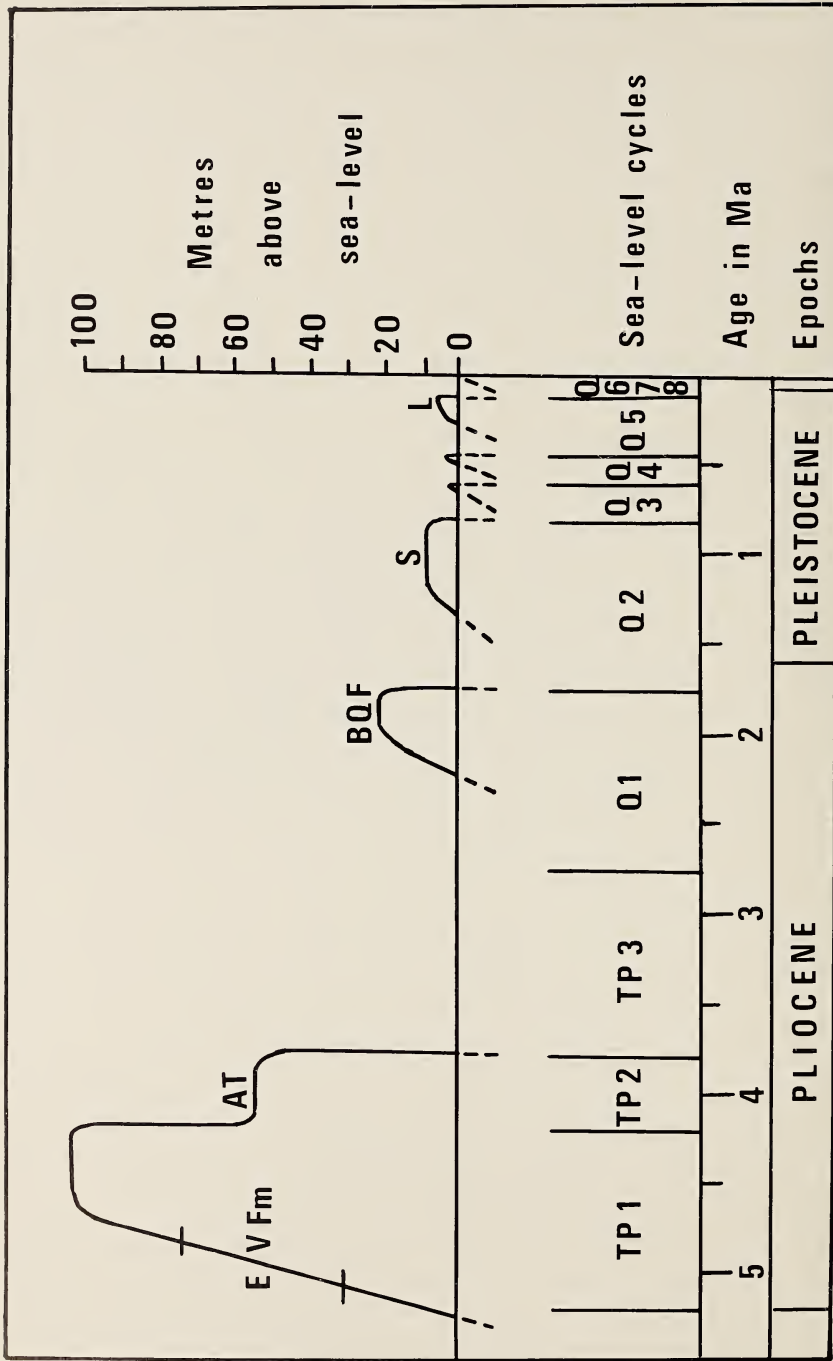


Fig. 17. Diagrammatic representation of sea-level changes indicated by features and deposits in the Saldanha region. (Adapted from Hendey 1981b, fig 4. EV Fm - 'E' Quarry, Varswater Formation; AT - Anyskop terrestrial deposits; BQF - Baard's Quarry fluvatile deposits; S - Skurwerug dune; L - Langebaan barrier. Tertiary sea-level cycles after Vail *et al.* 1977; Quaternary cycles after Beard *et al.* 1982.)

TABLE 4
Pliocene to Holocene high sea-levels in the Saldanha region.

<i>Feature/deposit</i>	<i>Location</i>	<i>Height of sea above present level</i>	<i>Age</i>	<i>Eustatic cycle</i>
Beach ridge	1 km east of Kreefbaai	1,5 m	Holocene	Q8
Beach deposits and wave erosion features	Langebaan barrier	3–4 m	late Pliocene (Eemian, 5c) 125 ka	Q5
Coastal dune and wave-cut platform	Skurwerug	7–8 m	early Pliocene 0,8–1,3 Ma	Q2
Submarine platform	Inland from Skurwerug	c. 20 m	late Pliocene 1,75–2,05 Ma	Q1
Fluviatile deposits	Baard's Quarry, Langebaanweg			
Coastal dune	Anyskop, Langebaanweg	c. 50 m	middle Pliocene 3,8–4,2 Ma	TP2
Marine deposits	Groot Springfontein			
Erosion surfaces	Varswater, Witteklip, etc.			
Submarine platform (on Varswater Fm)	Elandsfontein	c. 100 m	early Pliocene 4,2–5,2 Ma	TP1
Paralic deposits (Varswater Fm)	'E' Quarry, Langebaanweg			

References: Pliocene—Hendey (1981a, 1981b); Late Pliocene/Holocene—this paper.

The Skurwerug *Kolpochoerus* and dune have other palaeoenvironmental implications. The dune itself is similar in some respects to the nearby Spreeuwal dune complex on the present shoreline of Saldanha Bay. The latter has been described by De la Cruz (1978) and it is similar to the series of 'dune plumes' on the Cape west coast discussed by Tankard & Rogers (1978), Rodrigues (1978) and Rogers (1982). It is a relatively small example of a dune plume and is situated adjacent to the beach on the north-eastern shore of Saldanha Bay. The Spreeuwal plume is not entirely unvegetated as indicated by Hendey (1983a, fig. 3), but consists of a complex of vegetated parabolic dunes, with 'hairpin' extensions inland that have a south to north orientation determined by the prevailing dry-season (summer) winds (Fig. 16). There are, however, some patches of unvegetated barchanoid dunes superimposed on the vegetated dunes. The largest

of the 'hairpin' dunes is the most easterly, and it has a maximum height of about 40 m and a length of a little over 2 km. The relatively small size of this plume is evidently due to the restricted sediment supply in Saldanha Bay, which is now unconnected with the only large river in the area (i.e. the Berg River, which discharges into St. Helena Bay). The largest of the west-coast plumes are situated north of river mouths, where fluvial sediments provide replenishment for the dunes (Tankard & Rogers 1978).

At least three phases of dune activity are evident in the dune plumes of the Cape west coast. The youngest dunes are active today and are clearly influenced by existing sea-level and climatic conditions. The dating of the two earlier phases of dune activity is by inference only. The partly vegetated dunes have been correlated with the Flandrian transgression (Rodrigues 1978), and regarded as the local equivalent of the 'Flandrian Episode I' dunes on the Californian coast (Cooper 1967), an area that is environmentally similar to the Cape west coast. The oldest dunes, which are completely vegetated, may be the local equivalent of the 'pre-Flandrian' dunes of California, and they may well date back to the highest of the sea-level stands during the Eemian interglacial (i.e. during oxygen isotope substage 5e).

The Skurwerug dune represents the vestiges of a dune plume that was apparently developed under similar circumstances during the 7–8 m high sea-level of the early Pleistocene. Judging from the remnants of this dune, its easterly parts at least must have been very like the easterly 'hairpin' dunes of the Spreewal plume in terms of orientation, height and length. This suggests that the climatic conditions that prevailed during the period of development of the Skurwerug dune (i.e. eustatic cycle Q2) must have been similar to those later in the Quaternary that influenced the formation of the Spreewal plume (i.e. cycles Q5 and Q8). Given the well-documented cyclicity of climates during the Quaternary, this is not unexpected, but the Skurwerug dune is significant in having provided the first direct evidence of the nature of early Pleistocene climate in the southwestern Cape.

The similarity in the sizes of the Spreewal and Skurwerug dunes is also significant in suggesting that the sediment supply in Saldanha Bay was as restricted during the early Pleistocene as it was during the late Pleistocene and Holocene. It follows that the Berg River must already have been following its present course by the early Pleistocene, and that the last time it could have discharged into Saldanha Bay was during the 20 m stillstand of the late Pliocene (Hendey 1981a). The exclusively marine nature of the sediments that underlie the 12 m platform inland of Saldanha Bay (Rogers 1983) is a further indication that the Berg River had diverted to a more northerly course by the end of the Pliocene.

It has already been indicated elsewhere that the Skurwerug *Kolpochoerus*, and the other mammals recorded from this locality, provide evidence that the local vegetation in their lifetimes differed from that of the present (Hendey 1983b). Although the habitat preference of *Kolpochoerus* cannot be precisely defined, this genus is likely to have inhabited fairly densely vegetated areas, since

its dentition is more like those of the living forest hog and bushpig than that of the open-country warthog. The present strandveld and fynbos vegetation communities of the Saldanha region are clearly unsuitable habitats for Suidae, and it is likely that at least some forested or wooded patches still existed in this region during the early Pleistocene. Furthermore, even though they may not have been contemporaries of the *Kolpochoerus*, the grazers represented in the Skurwerug deposits (i.e. *Equus*, *Connochaetes*, *Gazella*) support the view that grasses were more prominent in the Pleistocene vegetation communities of the south-western Cape than is the case today (Hendey 1983b). The present vegetation communities of the Cape west coast are clearly not a prerequisite for the formation of the coastal dune plumes.

To sum up, the discovery of the Skurwerug *Kolpochoerus paiceae* skull was a fortunate event for a variety of reasons. Not only has this fine specimen shed further light on the history of *Kolpochoerus* in South Africa, it has also resulted in further support for the correlation of the west-coast late Cenozoic succession with global sea-level changes. In addition, by indicating the likely age of the Skurwerug dune, it has led to the conclusion that local climatic conditions during the early Pleistocene were at least in some respects similar to those later in the Quaternary. Finally, it adds to the growing body of evidence that Pleistocene vegetation communities of the south-western Cape coastal plain were generally very different from those of the present.

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